Plant-parasitic Nematodes in Canada

Part 1

An illustrated key to the genera

Errata for

Plant-parasitic Nematodes in Canada Part 1 An illustrated key to the genera

by
R V. Anderson and R. H. Mulvey
Biosystematics Research Institute
Ottawa, Ontario

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Page 21, Key No. 5, right-hand column: Add 6

Page 22, Key No. 10, right-hand column: For . . . . 34 read 19

Page 59, caption for Fig. 20.5, line 1: For Nothocrinconema read Nothocriconema

Page 65, caption for Fig. 26, line 2: For Northocroconema read Nothocriconema

Page 65, caption for Fig. 26, line 5: For Nothocrinconema read Nothocriconema

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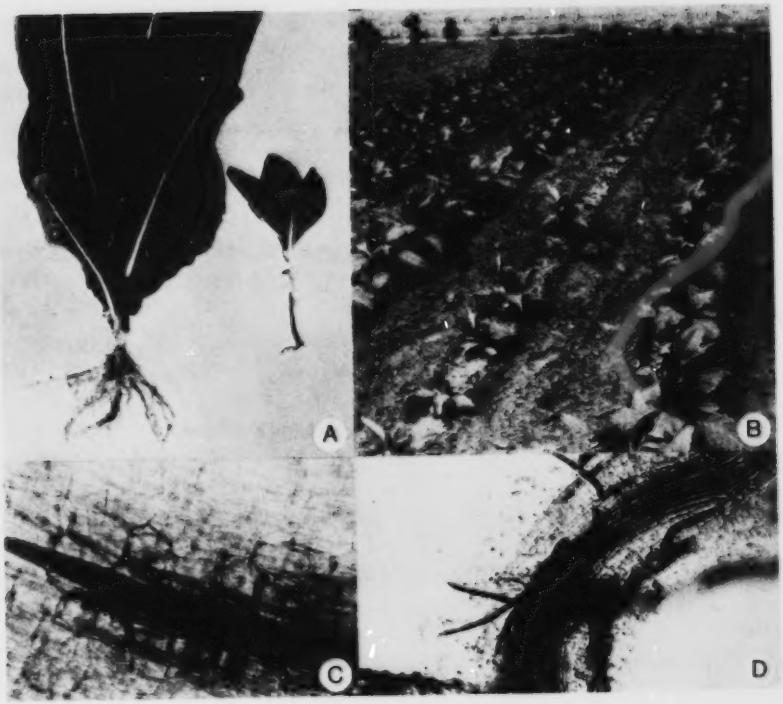
Part 1



Frontispiece: Photographs illustrating some of the characteristic damage caused by plant-parasitic nematodes on crops.
Upper left. A healthy tobacco plant (*left*) contrasted with a diseased plant (*right*) of the same age attacked by the root-lesion nematode, *Pratylenchus neglectus*. Plants that are stunted by severely injured root systems are evidence of the destruction caused by plant-parasitic nematodes.
Upper right. Selective soil fumigants (nematocides) are sometimes used to alleviate nematode damage to cash crops in the field and greenhouse. The center row of tobacco planted in nonfumigated soil contains missing and stunted plants, and contrasts sharply with adjacent rows of uniform, healthy plants growing in fumigated soil.
Lower left. The discoloration and death of cortical cells around this single root-lesion nematode in a feeder root is a characteristic reaction to attack by nematodes.
Lower right. The localized invasion of roots by migratory nematodes creates large, blackened lesions that may ultimately fracture or break the root.
Photographs by W. B. Mountain, courtesy of J. L. Townshend, Research Branch, Agriculture Canada, Vineland Station, Ont.

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R. H. Mulvey

Biosystematics Research Institute
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Preface

A large and thriving community of diminutive roundworms, or nematodes, lives within the soils of Canada. A few grams of soil from a garden, lawn, forest, or farm may contain scores of individual nematodes. Because of their transparent bodies and small size (seldom exceeding 2 mm in length and 0.04 mm in width), special extraction techniques are necessary to detect their presence in the soil. When they are isolated in a clear water suspension and observed under a microscope, a mixture of species appears that exhibits great diversity in form and purpose. Some kinds are highly adapted to feeding on microorganisms or the decomposition products of animals and plants; other species prey on other nematodes and on small invertebrates; occasionally they are parasites of insects; and, invariably, some species attack plants. Nematodes themselves may also be victims of fungal, viral, bacterial, protozoan, or invertebrate parasites. Consequently, the existence of nematodes in faunal communities is important for sustaining the structure and viability of the soil ecosystems. To the grower, however, nematodes are pests that create problems in plant management and production, particularly of nursery and agricultural crops.

The economic importance of plant nematodes in Canada was first recognized in the early 1930s with the discovery of the bulb and stem nematode, which attacks flower bulbs in Western Canada. Subsequently, losses severely affecting the value and quality of other crops were recorded, including table and certified seed potatoes attacked by the potato rot nematode (*Ditylenchus destructor*) in Prince Edward Island and by the golden nematode of potatoes (*Globodera rostochiensis*) in Newfoundland and Victoria, B.C.; ornamental bulbs, forages, and strawberry by the bulb and stem nematode (*Ditylenchus dipsaci*) in Western Canada; tobacco and peach trees in southern Ontario and forage crops in Eastern Canada by the root-lesion nematode (*Pratylenchus penetrans*); sugar beets by the sugarbeet nematode (*Heterodera schachtii*) in southern Ontario; hothouse vegetables and some field crops by the northern root-knot nematode (*Meloidogyne hapla*); and the foliage of ornamentals, such as chrysanthemum and begonia, and strawberries by foliar nematodes (*Aphelenchoides ritzemabosi* and *A. fragariae*). By 1950, it had been firmly established that the destructiveness of plant-parasitic nematodes was not restricted by crop, provincial boundaries, or to a few nematode species. From systematic soil surveys, more than 200 species of plant-parasitic nematodes are now known to occur in Canada and this number is always increasing.

Because most parasitic nematodes attack the roots of plants, the disease symptoms, as expressed in appearance and vigor of the plant, are not definitive and have little diagnostic value. Furthermore, not all nematodes have the potential to kill or significantly limit the production of plants. The recognition and accurate identification of the economically important nematodes is therefore essential in order to detect and assess nematode disease problems and to implement effective control and regulatory measures.

This illustrated key to the genera of plant-parasitic nematodes in Canada will acquaint growers and specialists concerned with the cultivation and production of healthy plants with the kinds of soil-inhabiting nematodes that attack plants. It is based largely on the Canadian National Collection of Nematodes, a repository of more than 100 000 labeled specimens collected from soil and plants throughout Canada in the past 25 years. About 50% of the total world genera of plant-parasitic nematodes are represented, which include about 10% of the total known species. The key will aid in identifying Canadian genera, and it will also serve as a guide and basic reference for a subsequent series of keys to be published on the species of plant nematodes by family groups.

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Introduction

The genera in this key contain species that are obligate parasites and therefore require a living food source to survive and propagate. Most nematodes feed exclusively on the cells of vascular plants, but some species that are common in the genus *Ditylenchus*, the family Aphelenchoididae, and the superfamily Neotylenchoidea feed partly or solely on soil fungi. The genus *Seinura* contains species that are predators of other nematodes and is included in the key because it occurs with, and is morphologically similar to, other genera in the suborder Aphelenchina. For other species in many of these genera, the food requirements and habits are yet unknown. Canadian species and groups of species that have proven economic importance are listed by common name in the glossary.

The genera of nematodes classified as plant parasitic have common parasitic characteristics, which distinguish them from many of the free-living, nonparasitic soil inhabitants. Most importantly, they all have an axial, protrusible stylet or "spear" in the head end that serves as a useful marker for their initial separation. In the suborders Tylenchina (Figs. 1–70) and Aphelenchina (Figs. 71–78) and the family Longidoridae (Figs. 79–82), the stylet is tubular. It is used to puncture the plant cell wall by a series of rapid thrusts, to withdraw the cellular contents, and in the Tylenchina, to inject salivary secretions when it is necessary to predigest the cellular contents prior to ingestion. In the family Trichodoridae (Figs. 83–85) the distinctive, arcuate stylet is not hollow and serves only to rupture a root cell, thereby releasing its contents into the mouth cavity of the nematode. Although many of the commonly occurring nonplant-parasitic species are readily recognized by the absence of a stylet, some having a stylet (*see* Fig. 79*A*, *D*) may be confused with plant parasites. The representative kinds of stomatostyles (order Tylenchida), odontostyles (family Longidoridae), and onchiostyles (family Trichodoridae) illustrated in this key will aid in the separation of these species. After the plant-parasitic species have been sorted from a mixed soil population, the key and labeled illustrations can be consulted to determine the genus. To emphasize and clarify their natural relationships in form and structure, the genera of Canada have been organized into family groups.

Collecting and Preparing Nematodes

Collecting and identifying the genera of plant-parasitic nematodes are necessarily limited by the availability of proper laboratory and microscope facilities and by the technical difficulties of handling and preparing nematodes for study. With experience, many of the genera and families can be recognized in a water suspension at the magnifications of a dissecting microscope. Some of the genera and most species, however, require examination of mounted specimens at the magnifications of a research microscope to observe the minute diagnostic features. Some methods of general applicability for collecting and extracting nematodes from soil and plant tissue and the laboratory procedures and equipment for handling and mounting them are considered in this publication. A more comprehensive guide to conventional nematological methods can be found in the list of general references.

Collecting and carrying infested soil and plant material

A convenient method of collecting soil samples is with a garden trowel or a small-bladed shovel. Soil samples should be 15–20 cm deep. When you collect a plant that you suspect is a host, be sure to include also a portion of the root system and some of the diseased foliage. The whole sample should be about 1 L in volume. When you are sampling a large area, take several random samples to obtain a reliable estimate of the species present. If you are collecting samples from diseased areas, be sure to include some soil from diseased as well as adjacent healthy-looking plants. Do not collect from dead plants.

After you have collected the soil sample, place it in a watertight container. Recovery of active nematodes may be greatly reduced if the soil is allowed to dry out or is kept at temperatures higher than soil conditions in the field. A polyethylene bag is the most suitable container for storing and carrying soil samples. If you have to keep the samples for a long time, store them in a refrigerator or a cold room at about 4°C.

Extraction methods

There are many methods with various modifications for extracting nematodes from soil and plant material. The selection of any one method depends largely on the degree of accuracy required in assessing the kinds

and numbers of nematodes in a specific habitat and type of soil. Only a few of the more conventional methods having broad application and requiring a minimum of equipment and effort are described in this publication.

Baermann funnel technique. The Baermann funnel technique is a simple and convenient method for extracting soil nematodes. It requires a minimum of time and equipment. This method allows you to make a fair assessment of the kinds of nematodes present, but it is not reliable for quantitative determinations.

The equipment is a 15 cm glass or plastic funnel, fitted with a short length of rubber tubing that closes by means of a spring or screw clamp. Add water until the level is about 2.5 cm below the funnel rim. Place a 10-mesh copper screen disk at the water level and a sheet of wet-strength facial tissue on the supporting screen. Carefully place soil, roots, pieces of foliage, or bark on the tissue and allow them to stand undisturbed for about 12 h or overnight. Some species will die and deteriorate if they are left longer than that in the funnel. The active nematodes move through the tissue, leaving the debris behind, and they may be collected in a small dish of clear water.

Cobb sifting and gravity method. The Cobb sifting and gravity method is widely used for extracting nematodes from soil and freshwater habitats.

This method, and its various modifications, is useful for processing large quantities of soil in the laboratory. It offers more reliable quantitative and qualitative data than the Baermann funnel technique. Nematode counts, however, are not as reproducible with this method as with other more sophisticated extraction methods, and the heavier clay soils and peats are harder to process.

The equipment consists of a series of copper or stainless steel screens of 10, 25, 100, 200, and 325 mesh, two 9 or 13.6 L buckets, a 15 cm funnel, and several 250 mL beakers. Place about 1 L or less of soil in a bucket and thoroughly mix it with about three times as much water and break up all the lumps. First, pour the soil suspension through the 10-mesh screen to remove the organic debris. Discard the heavier soil particles at the bottom of the bucket and the residue from the 10-mesh screen. Then pass the soil suspension through each of the remaining screens, allowing a few seconds between screenings to settle the heavier particles for discard. To collect the nematodes and soil particles of similar diameter from the 25-, 100-, 200-, and 325-mesh screens, gently wash the residue to one side of the screen and into 250 mL beakers. Use a fine stream of water from a plastic squeeze bottle or small hose for this purpose. To prevent contamination, thoroughly wash the screens with hot water before reusing them.

Put the residue collected from each screen in a bulk container, or if you are interested in nematodes of specific size, keep each screening separate. To

further concentrate the nematodes, fill each beaker with water and allow the nematodes to settle undisturbed for about 1 h. Then quickly decant the supernatant to half volume. Except with sandy soils, the nematode suspensions require further clearing before you can observe them directly. To do this, carefully pour the suspension and the remaining soil particles on tissue in a Baermann funnel or cover the mouth of the beaker with a sheet of tissue or muslin cloth, firmly held with a rubber band, and invert the beaker in a funnel of water.

Centrifuge–flotation. The centrifuge–flotation method is a quick and effective way of extracting nematodes from most types of soil. The nematode population is better collected by this method than by most other methods, because of the greater recovery of living as well as inactive and dead specimens.

A simplified procedure is to place a 100–150 cm^3 aliquot of soil in a 10-mesh screen or kitchen sieve. Wash the soil through the screen into a bucket with a dispersed stream of water. Collect nematodes on a 325-mesh screen and wash them into a 250 mL beaker, as described in the Cobb sifting and gravity method. Add the suspension of nematodes to centrifuge tubes, add water for balance, and spin for 2–3 min at 2000 rpm. Discard the clear supernatant and replace it with a sugar solution prepared by dissolving 0.45 kg of sugar in 1000 mL of water. Stir the nematodes and soil particles from the bottom into suspension and respin them for 2–3 min at 2000 rpm. Then pour the supernatant containing the suspended nematodes into the corner of a tilted 325-mesh screen and gently wash them from above to remove the sugar. After a few seconds of rinsing, tilt the screen forward and wash the nematodes into a watch glass for direct observation. Some of the species tend to collapse while they are in the sugar solution, but they soon become turgid and active in clear water.

Extracting nematode cysts. The economically important cyst-forming species of the genera of Heteroderidae require special techniques to recover the adults for identification. Unlike most plant nematodes, their bodies becomes spherical at maturity and are transformed into hardened egg-carrying shells. Because the cysts are inactive and tend to float in water, they may escape detection by the conventional extraction methods. Usually they are recovered more easily from dried soils than from moist field soil.

A simple method of detecting and isolating cysts is to place a 250 cm^3 sample in a 2 L Erlenmeyer flask. Cover the soil with water, shake the soil and the water together vigorously, and add more water, filling the flask to the brim. Allow 15–30 min for the cysts to rise, then carefully pour the flotsam over a double set of 20- and 60-mesh screens. Gently wash the flotsam on the 20-mesh screen through to the 60-mesh screen with a dispersed stream of water. Wash the remaining debris and cysts off the screen into a 15 cm funnel lined with a moistened filter-paper cone. Pick the cysts directly off the filter paper with the aid of a dissecting microscope.

More elaborate cyst-extracting equipment is available for handling larger volumes of soil required in surveys.

Preparing nematodes for identification

Nematodes are usually collected individually and sorted from mixed populations in clear water before they can be identified. A dental pulp canal file or sharpened bamboo splinter is useful for this purpose. With few exceptions, most nematodes are 2 mm or less in length and they are easiest to work with at magnifications of X40 or more. Identifications are based primarily on the adult. The immature forms usually do not have enough characteristics to enable specific determinations.

Killing. The identification of nematode species is based largely on minute external and internal characteristics. Because of their delicate tissues and lack of a skeletal or structural frame, the method of killing and fixing is critical. Specimens killed in cold or most hot fixatives become too distorted to be identifiable.

The safest method of killing mixed populations is by slowly passing a glass slide or dish with the nematode suspension over a small alcohol flame. Examine the nematodes from time to time until all movement has stopped and they have assumed a relaxed, undistorted posture. To ensure a complete kill, allow the suspension to cool to room temperature and then watch for movement after a few minutes.

Fixing. The cellular contents of heat-killed specimens soon begin to deteriorate in water unless they are fixed immediately. For most purposes, a 2–4% solution of formalin satisfactorily preserves tissues.

Preparing nematode mounts

Permanent whole mounts of nematodes are usually placed in pure glycerol and are either mounted on glass slides or sealed between double cover slips mounted in Cobb aluminum slides. Aluminum slides allow you to study both sides of the nematodes at high magnifications and they are less likely to break than glass slides. Nematodes mounted in glycerol last indefinitely, retaining good structural and optical quality.

Seinhorst's glycerol–ethanol method. Seinhorst's method is a quick and effective method for processing nematodes to pure glycerol. A few species tend to collapse if they are processed too rapidly in glycerol, and these require slower processing methods to complete the impregnation of body tissues.

Transfer the nematodes individually or in bulk from the fixative with a finely drawn pipette to a 1–2 mL solution containing 20 parts of 95% ethanol, 1 part of glycerol, and 79 parts of distilled water. A 3.9 cavity block or other small dish that holds about 5 mL is suitable for this purpose. Set the cavity block on a support in a small closed jar that contains about 1/10th its volume of 95% ethanol, and place it in an oven at 35–40°C. After about 12 h, the water has been replaced by ethanol, and the cavity block is then filled with a solution of 5 parts of glycerol and 95 parts of 95% ethanol. Then transfer the dish to a container or narrow preparation dish that is partly closed, to slow down evaporation of the ethanol, and maintain the temperature at 40°C for at least 3 h. The nematodes can then be permanently mounted or maintained in small vials of desiccated glycerin. A trace of copper sulfate or thymol may be added to the glycerin to prevent growth of molds.

Semipermanent lactophenol mounts. Good-quality mounts that will keep for several months can be prepared quickly in lactophenol. Transfer the heat-relaxed and fixed nematodes directly to hot lactophenol that has been heated slowly to 65–70°C. Keep the temperature steady for 2 or 3 min or until the nematodes have cleared sufficiently. Overheating thickens the lactophenol and may alter or distort important diagnostic features of the specimens. Light staining with lactophenol containing about 0.005% cotton blue may enhance the character and delineation of certain internal structures.

Preparing permanent slides

For making Cobb aluminum slides, use No. 0 square 25 mm and round 18 mm cover slips. Support the smaller top cover slip with fine glass rods slightly smaller in diameter than that of the nematodes. Glass rods of these diameters may be obtained from spun glass wool or may be drawn from heated glass tubing. Store the rods in desiccated glycerin and cut them to about 1 mm lengths when you need them.

Sort glycerin-processed specimens first by size and, if feasible, then by genus under the dissecting microscope. Transfer the nematodes individually to a small drop of glycerin on a square cover slip (Cobb slide) or a glass slide; center them and arrange them in rows. Place three glass rods of appropriate diameter equidistantly around the centered nematodes. For identification purposes, a slide should contain no more than 10 specimens. To avoid bubbles and excessive movement of nematodes, lightly heat the round cover slip top and carefully place (do not drop) it on the mounting drop. Carefully use the correct amount of glycerin so that it does not extend beyond the edge of the cover slip. To seal the slide, tack the cover slip to the slide at three points with a small drop of sealing cement called Zut (Glyceel in Europe). When the sealant sets, ring the mount on a turntable with a thick layer of cement applied with a small camel's-hair brush. This sealing compound contains a plasticizer that prevents the ring from cracking. Butyl acetate may be used to thin the cement if necessary.

Classification
Phylum
NEMATODA
(in part)

Taxon: Order (-ida) Suborder (-ina) Superfamily (-oidea) Family (-idae)	Key number	Reference
Tylenchida		B. 4, 10, 12
Tylenchina	1	B. 1, 5
Neotylenchoidea	3	B. 4, 12
Neotylenchidae	4	C. 1–4
Paurodontidae	7	C. 1–4
Nothotylenchidae	7	C. 1–4
Criconematoidea	10	B. 4
Paratylenchidae	11	C. 5–12
Criconematidae	11	C. 13–18
Tylenchoidea	10	B. 9, 10
Tylenchidae	19	C. 19, 20
Dolichodoridae	29	C. 21
Tylenchorhynchidae	29	C. 22, 23
Pratylenchidae	34	C. 24–27
Hoplolaimidae	34	C. 28–34
Heteroderoidea	2	B. 4
Meloidogynidae	40	C. 35
Heteroderidae	40	C. 36–40
Aphelenchina	1	B. 3
Aphelenchoidea	43	B. 4, 5, 11
Paraphelenchidae	43	C. 41–43
Anomyctidae	44	C. 41–43
Aphelenchoididae	44	C. 41–43
Aphelenchidae	46	C. 41–43
Dorylaimida		B. 2, 3, 5
Dorylaimina	47	B. 14
Dorylaimoidea	47	B. 1, 13
Longidoridae	47	C. 44–46
Diphtherophorina	47	B. 2
Trichodoroidea	47	B. 3, 5
Trichodoridae	47	C. 47, 48

Key to the Genera

Order Tylenchida

- Esophagus composed of a muscular procorpus, expanded metacorpus, narrow isthmus, and a glandular basal bulb of usually 3 cells (Figs. 2, 15, 16)
- Stylet (spear) a stomatostyle (Figs. 24, 64*D*)
- Esophageal glands emptying through long extensions into lumen in metacorpus or anteriorly in procorpus (Figs. 4*A*, *B*, *C*, *E*; 13*B*; 71*A*, *B*)
- Excretory system generally conspicuous; duct lining cuticularized, refractive (Fig. 13*D*, *E*)
- Cuticle annulated, with or without longitudinal striations and lacking cuticular pores (Figs. 1, 2, 3)
- Amphid apertures located on lips (Figs. 35, 53*A*, 65*C*, 67*A*); amphid pouches obscure
- Phasmids present, usually on or near tail (Figs. 47*F*; 58*A*, *B*, *C*, *D*; 61*E*)
- Female tails without caudal papillae and males lacking supplements or genital papillae

.... 1

Order Dorylaimida

- Esophagus composed of a narrow corpus and an expanded basal bulb containing usually more than 3 cells (Figs. 79*A*, 85*A*)
- Stylet (spear) an odontostyle or onchiostyle (Figs. 79*D*, 80, 85*D*)
- Esophageal glands emptying into lumen through short extensions in basal bulb, rarely into corpus
- Excretory system absent (Longidoridae) or, if present (Trichodoridae), generally obscure with duct lining weakly cuticularized
- Cuticle generally thick with smooth surface and containing numerous cuticular pores (Figs. 79, 82, 83, 84*B*)
- Amphid apertures located below the lips, near base of head; amphid pouches large (Figs. 79*B*, *C*, *D*; 85*B*, *C*)
- Phasmids absent
- Female tails bearing caudal papillae and males bearing supplements or genital papillae (Figs. 79*E*, 83*A*)

.... 47

1 .... Suborder Tylenchina

- Dorsal esophageal gland emptying into lumen of esophagus between the stylet and metacorpus (Figs. 4*A*, *B*, *C*; 64*D*)
- Metacorpus rarely occupying entire body cavity, with or without a well-developed valvular apparatus (Figs. 2; 4*A*, *D*; 10*A*; 13*C*)

.... 2

Suborder Aphelenchina

- Dorsal esophageal gland emptying into lumen of esophagus in anterior half of metacorpus (Fig. 71*A*)
- Metacorpus always well-developed, occupying the entire body cavity and containing a large, refractive valvular apparatus (Figs. 72, 73*A*)

.... 43

2 ....

- Adult females and males vermiform, motile (Figs. 7, 45)
- Ectoparasites and migratory endoparasites of vascular plants; some species mycophagus (Figs. 5, 7, 8)
- Eggs deposited in soil or plant tissue (Fig. 8)
- In males, spicules at least one body width anterior to tail terminus (Figs. 14*B*, *D*; 44*E*; 49*A*–*C*); bursa present or, in some Criconematoidea, absent (Fig. 20*C*)

.... 3

Superfamily Heteroderoidea

- Adult females saccate, nonmotile (Figs. 64*C*, 66*B*) males vermiform
- Sedentary endoparasites; females sessile on or in roots (Figs. 64*A*; 66*A*, *C*)
- Eggs deposited in a gelatinous matrix or retained within a cyst (Figs. 64*A*, 68*A*)
- In males, spicules at tail terminus; bursa absent (Fig. 67*C*, *D*, *E*)

.... 40

3 .... Superfamily Neotylenchoidea

- Metacorpus reduced, lacking a valvular apparatus (Figs. 9*C*; 10*A*; 13*A*, *B*)
- Females with one ovary (Fig. 16)

.... 4

- Metacorpus well-developed, containing a refractive valvular apparatus (Fig. 15)
- Females with one (Fig. 16) or two ovaries (Fig. 45)

.... 9

4 .... Family

Neotylenchidae

- Head skeleton divided into 8 sectors (Fig. 9*A*)
- Esophageal glands extending over intestine in long lobes (Fig. 9*B*, *C*), except *Neotylenchus* spp., which have not been found in Canada

.... 5

- Head skeleton divided into the typical 6 sectors (Fig. 12*A*)
- Esophageal bulb apposed to intestine or slightly overlapping; sometimes with a stem-like projection (Figs. 12*C*, *D*, *E*; 39)

.... 7

5 ....

- Esophageal glands obscure, not delineated from intestinal tissues
- Stylet shaft encircled by strengthening rings; stylet knobs bifid, slender

Hexatylus
(Fig. 10)

- Esophageal gland lobes well-defined (Fig. 12*C*, *D*, *E*)
- Stylet without strengthening rings; stylet knobs undivided (Fig. 11*A*)

6 ....

- Postuterine branch present (Fig. 11*D*)
- Vulva at about 80% of body length

Hadrodenus

- Postuterine branch absent (Fig. 11*C*)
- Vulva at about 90% or more of body length

Deladenus

7 .... Family

Paurodontidae

- Basal esophageal bulb with a stem-like projection (Fig. 12*C*)
- Stylet knobs at different levels (Fig. 12*B*)

Stictylus
(Fig. 12*B*, *C*)

Family

Nothotylenchidae

- Basal esophageal bulb cylindrical or pyriform, apposed to intestine (Fig. 12*D*, *E*)
- Stylet knobs opposite, uniformly rounded (Figs. 11*A*, 14*A*)

....8

8 ....

- Body (Figs. 43, 45) and tail (Figs. 19*B*, 34*A*) of female nearly linear or slightly curved
- Stylet knobs rounded (Fig. 14*A*)
- Bursa extending to near middle of male tail (Fig. 14*B*)

Nothotylenchus

- Body strongly arcuate (Fig. 16); female tail often hooked at terminus (Fig. 14*E*)
- Stylet knobs flange-like (Fig. 14*B*)
- Bursa of male short, adanal (Fig. 14*D*)

Boleodorus

9....

- Esophageal glands apposed to intestine (Figs. 15; 16; 21*A*, *B*) 10
- Esophageal glands overlapping intestine (Fig. 51) 34

10.... Superfamily Criconematoidea

- Procorpus expanded posteriorly, continuous with metacorpus (Fig. 16)
- Metacorpus massive, as large as or larger than basal esophageal bulb; containing a large, refractive valvular apparatus (Fig. 21*A*, *B*)
- Stylet apex at least 60% or more of total stylet length (Fig. 24)
- Anus obscure, often not discernible (Fig. 21*C*)
- Adult males underdeveloped; stylet reduced or absent and esophagus obscure; bursa absent, well-developed, or reduced (Fig. 20) 11

Superfamily Tylenchoidea

- Procorpus cylindrical or fusiform, set off from metacorpus (Figs. 2, 15*B*)
- Metacorpus smaller than basal bulb, with a moderately well developed valvular apparatus (Fig. 15)
- Stylet apex about 50% or less of total stylet length (Fig. 56*E*)
- Anus conspicuous (Figs. 47*B*, *D*, *E*; 54)
- Adult males well-developed, with a prominent stylet (Fig. 65*A*, *B*); bursa well-developed (Figs. 11*B*; 14*B*, *D*; 49*A*, *B*) 34

11.... Family Paratylenchidae

- Annules on head and body regular, less than 2 μm wide (Figs. 2, 35*A*, 56)
- Isthmus long and slender (Fig. 16)
- Basal esophageal bulb rounded or pyriform (Figs. 15, 16)
- Lateral vulval membranes present (Fig. 19*B*, *C*)
- Tail (vulva to tail terminus) shape conoid to elongate-conoid (Fig. 19*A*, *B*) 12

Family Criconematidae

- Annules on head and body very coarse, usually more than 3 μm wide (Fig. 26*A*, *B*, *C*)
- Isthmus short (Fig. 21*A*, *B*)
- Basal esophageal bulb reduced
- Lateral vulval membranes absent (Figs. 21*C*, 25*F*)
- Tail (vulva to tail terminus) short, conoid, often with a blunt terminus (Figs. 21*C*, 27*D*) 13

12 . . . .

- Stylet short and robust; if long always occupying much less than one-fourth of body length (Figs. 16; 18*C*, *D*)
- Excretory pore and hemizonid posterior to metacorpus (Fig. 19*F*)

Paratylenchus
(Fig. 16)

- Stylet long and slender, occupying at least one-third of body length (Figs. 17; 18*A*, *B*)
- Excretory pore and hemizonid at level of metacorpus or anterior (Fig. 19*D*, *E*)

Gracilacus
(Fig. 17)

13 . . . .

- Body annules with smooth, irregular or crenate margins (Fig. 22)

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- Body annules elaborately ornamented (Figs. 25–32)

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14 . . . .

- Cuticle of adult double

Hemicycliophora
(Figs. 23, 24)

- Cuticle of adult single (Figs. 21*A*, 25)

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15 . . . .

- Stylet very long, slender, flexible, occupying about 40% or more of total body length

Xenocriconemella
(Fig. 25*A*, *B*, *C*, *D*, *F*)

- Stylet length less than 40% of body length, typically robust and rigid (Figs. 1, 29*A*)

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16 . . . .

- Head bearing 6 small, uniform lips (pseudolips) (Fig. 26*A*), not reduced to lobes
- First head annule continuous, not divided (Fig. 26*A*)
- Anterior vulval lip large, often overlapping gonopore (Fig. 26*D*)

Nothocriconema
(Figs. 5, 20.5, 26)

- Head having greatly reduced and modified lips (Fig. 27*A*)
- Submedian lips in the form of lobes; lateral lips absent
- First head annule divided into labial plates
- Vulva open; vulval lips uniform (Fig. 27*D*)

Macroposthonia
(Fig. 27)

17 . . . .

- Body annules bearing long, transparent membranes (may be obscure or absent in fixed specimens) (Fig. 28)

Bakernema
(Fig. 28)

- Body annules bearing scales or spines (Figs. 29, 30, 31, 32)

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18 . . . .

- Head with submedian lobes (Fig. 30*A*)
- Body annules marked by scales arranged in longitudinal rows (Fig. 29)

Criconema
(Figs. 29, 30)

- Head apex typically dome-shaped bearing 6 liplets (Fig. 31*A*)
- Body annules with spines arranged in a continuous series or grouped in longitudinal rows (Figs. 31, 32)

Crossonema
(Figs. 31, 32)

19 . . . . Family

Tylenchidae

- Mostly small, fusiform species having delicate features (Fig. 33)
- Head skeleton obscure or weakly developed (Fig. 34*B*, *C*, *D*, *E*)
- Stylet small, about 9–13 μm long, with or without basal knobs
- Ovary single, anterior to vagina (Fig. 33)
- Tail shape ranging from conoid to filiform (Figs. 33, 34*A*)

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- Robust, cylindroid species having generally coarse, refractive features (Figs. 45, 60)
- Head skeleton usually well developed and refractive (Fig. 56)
- Stylet typically robust, over 15 μm long, with prominent basal knobs (Figs. 53, 56)
- Two ovaries, outstretched with one anterior and one posterior to vagina (Figs. 43, 45)
- Tails mostly subcylindrical with bluntly rounded termini, rarely conoid (Figs. 46*C*; 47*B*, *C*)

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20 . . . .

- Amphid apertures appearing as small obscure openings on head apex near oral opening (Fig. 35*A*)

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- Amphid apertures conspicuous, oval or elongate, and sited on sides of lips (Fig. 35*B*, *C*, *D*)

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21 . . . .

- Germinal cells (oogonia and oocytes) arranged in ovary in multiple rows around a rachis (Fig. 36*A*, *B*)
- Columella of more than 4 columns of cells (Fig. 36*C*)

Anguina

- Germinal cells typically in a single row or in tandem (Fig. 37)
- Columella (quadricolumella) composed of 4 columns of 4 cells (Fig. 36*D*)

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22 . . . .

– Head usually not annulated (Fig. 34*D*)
– Spermatheca tubular; sperm enclosed by a cytoplasmic membrane-bound layer (Fig. 38*A*, *B*)
– Tails conoid (Fig. 34*A*)

Ditylenchus

– Head usually annulated (Fig. 34*C*)
– Spermatheca saccate; sperm not enclosed by cytoplasm (Fig. 38*C*, *D*)
– Tail mostly elongate, conoid, or filiform (Fig. 33)

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23 . . . .

– Head with 4 prominent lips; lateral lips reduced (Fig. 40*A*, *B*, *C*)
– Lateral field with 2 incisures (Fig. 40*D*)

Ottolenchus
(Fig. 40*A*, *B*, *C*, *D*)

– Head with 6 characteristic, symmetrical lips (Fig. 35*A*)
– Lateral field with more than 2 incisures (Fig. 48)

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24 . . . .

– Head skeleton comprised of finger-like projections (Fig. 40*J*)
– Cuticle often loosely adhering to body

Dactylotylenchus
(Fig. 40*J*)

– Head skeleton normal, usually weakly developed and obscure (Fig. 34*B*, *C*, *D*, *E*)
– Cuticle of body not expanded or separated from body (Fig. 40*A*)

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25 . . . .

– Head rounded, set off from body (Fig. 40*H*)
– Lateral field with 6 incisures (Fig. 40*I*)

Cephalenchus
(Fig. 40*H*, *I*)

– Head continuous with body contour (Fig. 40*E*)
– Lateral field with 4 incisures (*see* Fig. 48*B*)

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26 . . . . .

– Body cuticle coarsely annulated, sometimes divided into blocks by longitudinal striae (Fig. 41*B*, *C*)
– Lateral vulval membranes present (Fig. 41*D*)

Aglenchus
(Fig. 41*A*, *B*, *C*, *D*)

– Body cuticle marked by regular annules (Fig. 41*E*)
– Lateral vulval membranes absent (Fig. 41*F*)

Tylenchus
(Fig. 41*E*)

27 . . . .

– Stylet with basal knobs (Fig. 42*A*)
– Dorsal gland orifice about 1 stylet length posterior to stylet (Fig. 42*A*)
– Tail always clavate (Fig. 42*B*)

Clavilenchus
(Fig. 42*A*, *B*)

– Stylet without basal knobs (Fig. 42*D*, *E*)
– Dorsal gland orifice usually near base of stylet, sometimes more posteriad (*see* Fig. 42*E*)
– Tail attenuated or clavate (Fig. 42*C*, *F*)

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28 . . . .

– Female with one ovary, prodelphic

Neopsilenchus
(Figs. 35*B*, *C*, *D*; 42*C*)

– Female with two ovaries, amphidelphic

Psilenchus
(Fig. 42*D*, *E*, *F*)

29 . . . . Family Dolichodoridae

– Large species more than 2 mm long (Fig. 43)
– Stylet length exceeding 80 μm (Fig. 44*A*, *B*)
– Bursa of male deeply cleft at tail terminus, dividing bursa into two large lobes

Dolichodorus
(Figs. 43, 44)

Family Tylenchorhynchidae

– Small species less than 2 mm long, mostly about 1 mm long (Fig. 45)
– Stylet less than 70 μm long, seldom exceeding 40 μm (Fig. 47*A*)
– Bursa of males normal, not lobed (Fig. 49*A*, *B*)

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30 . . . .

– Head skeleton obscure (Fig. 46*A*, *B*)
– Female with 1 anterior ovary
– Vulva near midbody
– Tail clavate, cuticle at terminus greatly thickened (Fig. 46*C*)

Trophurus
(Fig. 46*A*, *B*, *C*)

– Head skeleton well-developed, refractive (Fig. 46*D*, *E*, *F*)
– Female with 2 outstretched ovaries (Fig. 45)
– Vulva at midbody
– Tail subcylindrical or conoid; cuticle at terminus not appreciably thickened (Fig. 47*C*)

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31 . . . .

– Perioral labial disk present (Fig. 46*D*)
– Lips on head well-separated, lobate (*see* Fig. 35*A*)

Geocenamus
(Fig. 46*D*, *E*)

– Perioral labial disk absent or obscure (Fig. 46*F*)
– Lips amalgamated, not separated by deep longitudinal striae

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32 . . . .

– Lateral field with 5 incisures (Fig. 48*C*)
– Female tail conoid (Fig. 47*E*, *F*)

Quinisulcius
(Fig. 48*C*)

– Lateral field with 3, 4, or 6 incisures (Fig. 48*A*, *B*, *D*)
– Female tail subcylindrical, cylindrical (Fig. 47*B*, *C*, *D*)

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33 . . . .

– Lateral field with 3 or 4 incisures (Fig. 48*A*, *B*)
– Spicules with a velum (Fig. 49*C*, *D*)
– Gubernaculum linear (Fig. 49*A*, *D*)

Tylenchorhynchus
(Figs. 45; 47; 48*A*, *B*; 49)

– Lateral field with 6 incisures (Fig. 48*D*, *E*)
– Spicules lacking a velum; distal ends blunt, indented (Fig. 50*C*)
– Gubernaculum short, arcuate (Fig. 50*A*, *B*)

Merlinius
(Fig. 50)

34 . . . . Family Pratylenchidae

– Head low, flattened or broadly rounded (Fig. 53*A*, *B*, *C*, *D*)
– Tail conoid; length about twice or more of the anal body width (Figs. 52, 54)

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Family Hoplolaimidae

– Head high, rounded or truncated (Figs. 53*E*, *F*; 56)
– Tail thick, short, length about equal to the anal body width (Fig. 57)

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35 . . . .

– Head low, broadly rounded (Fig. 53*D*)
– Male and female large, more than 1 mm long
– Tail length 4 times anal body diameter or more (Fig. 54*A*)

Hirschmanniella
(Figs. 53*D*, 54*A*)

– Head low, flattened (Fig. 53*A*, *B*, *C*)
– Adult usually less than 1 mm long (Fig. 52)
– Tail length about twice the anal body diameter (Fig. 54*B*, *C*)

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36 . . . .

- Female with 1 ovary, prodelphic (Fig. 52*B*)

Pratylenchus
(Fig. 52*B*)

- Female with 2 ovaries, amphidelphic (Fig. 52*A*)

Pratylenchoides
(Fig. 52*A*)

37 . . . .

- Phasmids small, pore-like (Fig. 58*A*, *B*)
- Head skeleton moderately well developed and refractive (Fig. 56*A*, *B*, *C*, *E*, *F*, *G*)

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- Phasmids or scutella large (Fig. 58*C*, *D*)
- Head skeleton massive and heavily sclerotized (Fig. 55)

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38 . . . .

- Esophageal glands extending over intestine ventrally and laterally (Fig. 58*E*)
- Esophagointestinal valve axial (Fig. 58*E*)

Helicotylenchus
(Fig. 60)

- Esophageal glands extending over intestine dorsally (Fig. 58*F*)
- Esophagointestinal valve ventrad to axis (Fig. 58*F*)

Rotylenchus
(Figs. 56*E*, 58*F*)

39 . . . .

- Stylet knobs rounded or indented on anterior surfaces (Fig. 61*A*, *B*)
- Phasmids opposite, sited near or on the tail (Fig. 61*E*)

Scutellonema
(Figs. 56*A*; 59; 61*A*, *B*, *E*)

- Stylet knobs with projections on anterior surfaces (Figs. 55*A*; 61*C*, *D*)
- Phasmids separated, with 1 anterior and 1 posterior to the vulva (Fig. 61*F*)

Hoplolaimus
(Figs. 7; 55; 58*C*, *D*; 61*C*, *D*, *F*)

40 . . .

Family Meloidogynidae	Family Heteroderidae
– Adult female cuticle thin, white; annules forming diagnostic perineal patterns at terminal end (Figs. 62, 64*C*)	– Adult female transformed into a thick-walled cyst, having no perineal patterns (Fig. 66*B*)
– Larvae 330–380 μm long (Fig. 63*A*)	– Fenestrated terminal area of female present and diagnostic (Fig. 66*D*)
– Stylet moderately sclerotized, 10–12 μm long (Fig. 63*B*)	– Larvae 400–600 μm long (Fig. 63*D*)
– Male with a distinct head cap and large amphid apertures (Fig. 65)	– Stylet heavily sclerotized, about 20–27 μm long (Fig. 63*C*)
– Eggs deposited in gelatinous matrix (Fig. 64*A*)	– Male without head cap; amphid apertures small (Fig. 67*B*)
– Causes galls on plant roots (Fig. 64*B*)	– Eggs usually retained within female body and cyst (Fig. 68*A*)
	– Causes no hypertrophy of root tissue (Fig. 66*A*, *C*)
Meloidogyne (Figs. 63, 64, 65)	41

41 . . . .

– Females and cysts generally lemon-shaped, with a posterior protuberance (Fig. 66*B*, *C*)	– Females and cysts spherical, oval, or pear-shaped, without a posterior protuberance (Figs. 68*A*, 70*A*)
Heterodera (Fig. 66*B*, *C*)	42

42 . . . .

– Cysts spherical (Fig. 68*A*)	– Cysts spherical, ovoid, or pear-shaped (Fig. 70*A*)
– Vulval fenestra much larger than anal fenestra (Fig. 68*D*, *E*)	– Vulval and anal fenestra of equal size (Fig. 70*B*, *C*)
– Perineal tubercles present (Fig. 69*A*, *B*)	– Perineal tubercles absent (Fig. 69*C*, *D*)
Globodera (Figs. 68; 69*A*, *B*)	*Punctodera* (Figs. 69*C*, *D*; 70)

Superfamily
Aphelenchoidea

43 .... **Family**
Paraphelenchidae

- Esophageal glands contained in a bulb apposed to intestine, not overlapping (Fig. 72*A*)
  Paraphelenchus
  (Fig. 72*A*)

- Esophageal glands extending posteriorly over intestine in long lobes (Fig. 72*B*)

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44 .... **Family**
Anomyctidae

- Head bulbous, bearing an elevated perioral ring (Fig. 73*B*)
  Anomyctus
  (Fig. 73*A*, *B*)

Family
Aphelenchoididae

- Head smoothly rounded, without a perioral ring (Fig. 73*C*)

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45 ....
- Tail filiform (Fig. 74*C*, *D*)
- Head skeleton lacking a sclerotized central tube (Fig. 74*B*)

Seinura
(Fig. 74)

- Tail conoid or cylindroid (Figs. 76*C*, 78*B*)
- Head skeleton with a refractive central tube (Figs. 73*C*, 78*A*)

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46 ....

Family
Aphelenchidae

- Tail conoid; terminus with one or more mucros (Fig. 76*D*, *E*, *F*, *G*)
- Stylet with or without knobs or thickenings (Figs. 76*B*, *C*; 78*A*)
- Lateral field with usually 4 or fewer incisures
- Males usually without bursa; gubernaculum absent (Fig. 76*D*)

Aphelenchoides
(Figs. 75, 76)

- Tail of female cylindrical; terminus bluntly rounded, without a mucro (Fig. 78*B*)
- Stylet without basal knobs or thickenings (Fig. 78*A*)
- Lateral field with 6 to 14 incisures (Fig. 78*D*)
- Males rare, having a well-developed ribbed bursa (Fig. 78*C*)

Aphelenchus
(Figs. 77, 78)

47 . . . .

Suborder
Doryaimina
Superfamily
Dorylaimoidea
Family
Longidoridae

- Body elongated, usually more than 1.5 mm long and strongly curved ventrally when relaxed (Fig. 81*A*)
- Stylet an odontostyle, prominently sclerotized and linear (Fig. 80)
- Lumenal lining of esophagus heavily cuticularized (Fig. 79*A*)
- Basal bulb of esophagus cylindrical, muscular (Fig. 79*A*)
- Tail longer than anal body width (Fig. 81*C*)

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Suborder
Diphtherophorina
Superfamily
Trichodoroidea
Family
Trichodoridae

- Body short and cylindrical, nearly linear when relaxed; body length usually about 1 mm or less
- Stylet an onchiostyle, slender and dorsally arcuate (Fig. 85*D*)
- Lumenal lining of esophagus not heavily cuticularized (Fig. 85*A*)
- Expanded base of esophagus (basal bulb) pyriform (Fig. 85*A*)
- Tail less than 1 anal body width long; anus at terminus (Fig. 85*E*)

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48 . . . .

- Stylet extension or shaft flanged (Figs. 81*B*, 82*B*)
- Guiding ring near base of stylet apex (Fig. 82*A*)
- Amphid apertures appearing as elongated slits (Fig. 79*B*, *C*)

Xiphinema
(Figs. 80; 81; 82*A*, *B*)

- Stylet extension without flanges (Fig. 82*D*)
- Guiding ring toward anterior, near head (Fig. 82*C*)
- Amphid apertures appearing as small, obscure pores

Longidorus
(Fig. 82*C*, *D*)

49 . . . .

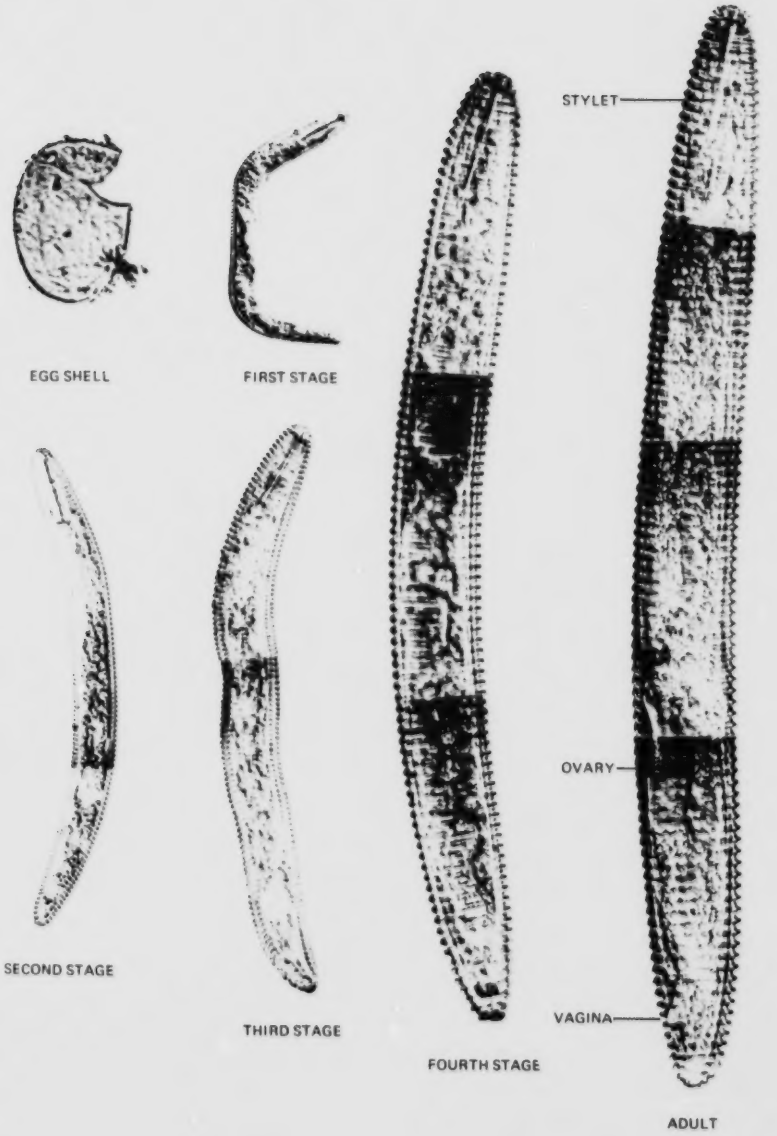
- Body cuticle becoming greatly distended after death of nematode (Figs. 83*C*, 84*B*)
- Vagina shorter than half the body width; vaginal walls thin (Fig. 84*A*)
- Male spicules slender, nearly linear (Fig. 83*C*)
- Spicular muscles (suspensors) linear, weakly developed (Fig. 83*C*)
- Male copulatory muscles absent anterior to spicules (Fig. 83*C*)

Paratrichodorus
(Figs. 83*C*; 84*A*, *B*; 85*A*)

- Cuticle not distended after death of nematode (Fig. 85*A*, *D*)
- Vagina long, extending more than half of body width (Fig. 84*C*)
- Male spicules arcuate (Fig. 83*A*, *B*)
- Spicular muscles well-developed, circular (Fig. 83*A*, *B*)
- Male copulatory muscles present anterior to spicules (Fig. 83*A*)

Trichodorus
(Figs. 83*A*, *B*; 84*C*)

Fig. 1. Life cycle of the ring nematode, *Macroposthonia xenoplax* (Criconematidae), representing the simple developmental stages of plant-parasitic nematodes. Development of the adult proceeds through 4 larval (juvenile) stages, each stage ending in a molt (*see* Figs. 53*C*, 80*C*) and the 1st stage occurring within the egg. The 1st stage larva shown was prematurely released by rupturing the egg under pressure. Generally, hatching is initiated by weakening the egg shell by repeated punctures with the stylet. After hatching, the larva is considered to be in the 2nd stage of development. Each stage is characterized by increments in body size and by increased development of the reproductive system. After the 4th and final molt, the nematode is in the adult or 5th stage and is capable of reproduction. Morphological characteristics of the adult are necessary for identification of plant parasites, whereas the characteristics of juveniles, except for some Heteroderoidea and Criconematoidea, have little diagnostic value. With sedentary endoparasites such as Heteroderoidea (*see* Fig. 63), the 2nd stage larva is the only infective stage, whereas in ectoparasites and migratory endoparasites (*see* Figs. 6, 7, 8), both the juveniles and the adults are capable of attacking plant tissue.


EGG SHELL
FIRST STAGE
SECOND STAGE
THIRD STAGE
FOURTH STAGE
STYLET
OVARY
VAGINA
ADULT

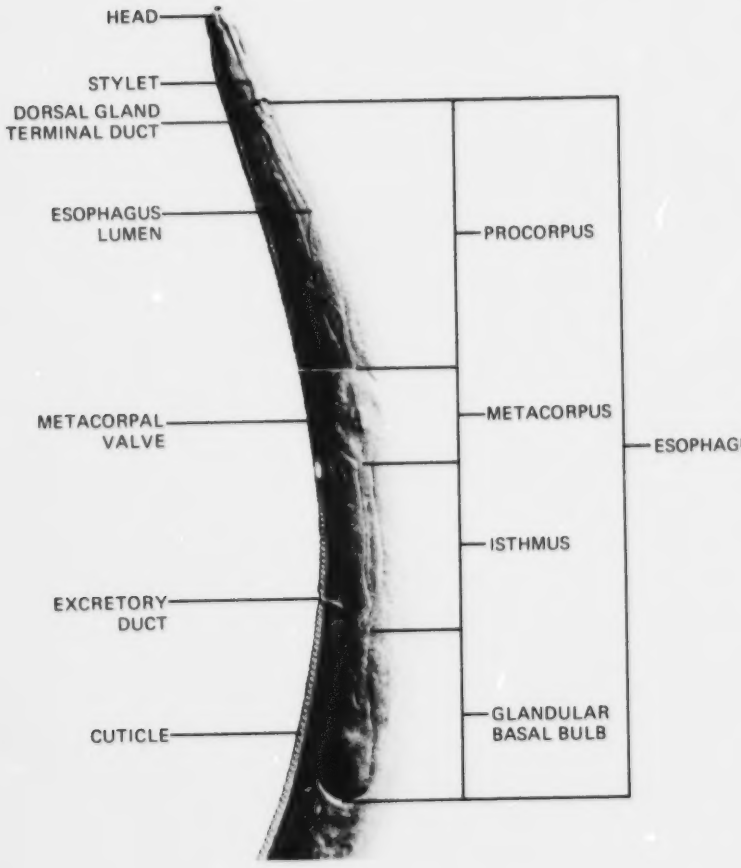


Fig. 2. Anterior end of *Quinisulcius acti* (Tylenchorhynchidae) showing the structure and form of the esophagus common to many plant-parasitic species. The esophagus is one of the most important diagnostic characters in the systematics and phylogeny of nematodes.

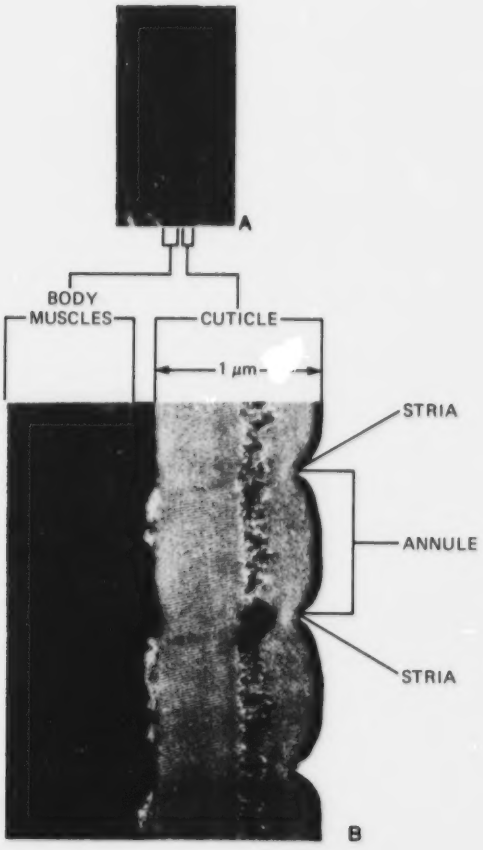
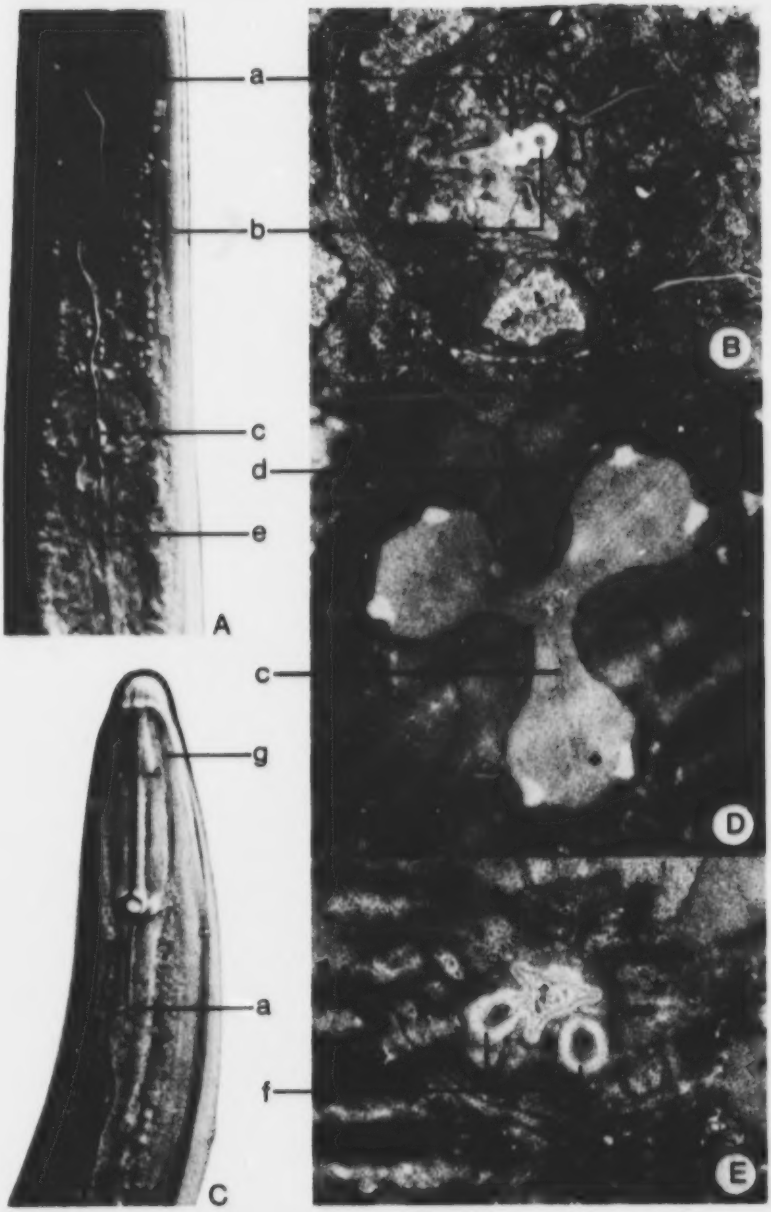


Fig. 3. Longitudinal section of the cuticle (exoskeleton) of a nematode seen through a light microscope (*A*) and through an electron micrograph (*B*) illustrating its complexity in structure. Although nematodes may sometimes appear to be segmented (*see* Fig. 20.5), the transverse striae dividing the cuticle into annules (*B*) extend into the outermost layers only. Some species also have longitudinal striae that intersect the transverse striae and divide the cuticle into blocks or plaques (*see* Fig. 41*B*, *C*).

Fig. 4. Gland orifices (terminal ducts) of the esophageal glands of nematodes in the suborder Tylenchina. *A*, Anterior portion of the esophagus of *Tylenchorhynchus dubius* showing the conspicuous dorsal gland orifice (*a*) which empties into the lumen (*b*) in the procorpus near the stylet (*a*). The two subventral glands empty through ampullae (*e*) and their ducts (not visible) into the lumen in the metacorpus posterior to the valve (*c*). *B*, Electron micrograph of a cross section at the junction of the dorsal gland duct (*a*) with the lumenal lining (*b*) of the esophagus. *C*, Lateral view through a light microscope of the junction of the dorsal gland with lumen of the esophagus in *Helicotylenchus platyurus*. Note the significantly more posterior position of the duct compared with the example in *A*. *D*, Electron micrograph of a cross section through the valvular apparatus (*c*) of the metacorpus. During feeding, when the nematode is ingesting contents of the food cell, the metacorpal valve rapidly opens and closes, and functions like a pump. Note the massive radial muscles (*d*) that control its action. *E*, Electron micrograph of a cross section at the posterior part of the metacorpus showing the junction of the subventral gland ducts (*f*) with the lumenal lining of the esophagus. Note that the lumen of the esophagus is triangular when viewed posteriorly to the metacorpal valve, but circular when viewed anteriorly (*B*).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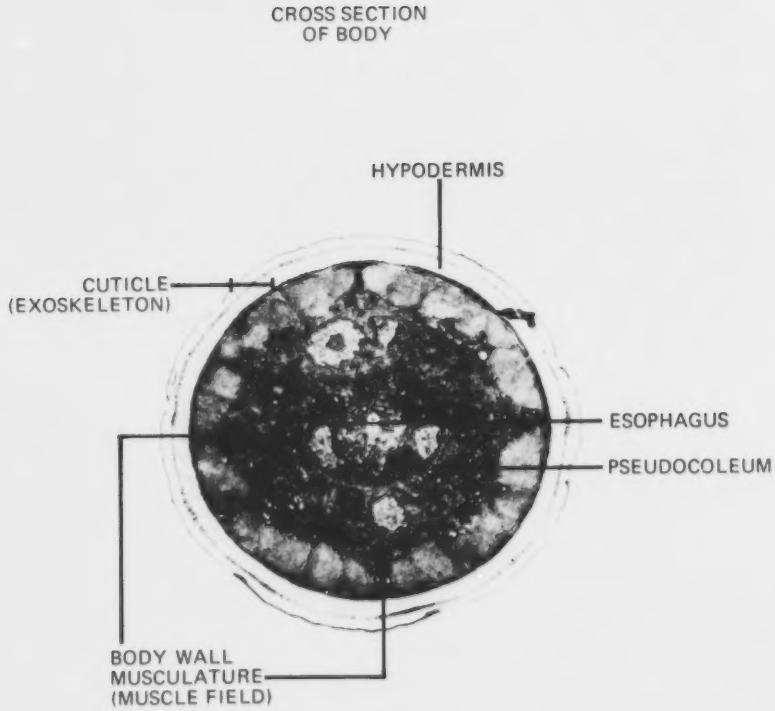


Fig. 5. Cross section (electron microscope) of the anterior end of a nematode illustrating characteristics of the phylum Nematoda (roundworms). The unsegmented, bilaterally symmetrical vermiform body consists of an outer body wall that surrounds a pseudocoelom, the tubular digestive tract, and the reproductive system (not shown). The body wall is composed of the cuticle (exoskeleton), hypodermis (epidermis), and fields of longitudinal, somatic muscle cells that control body movement.

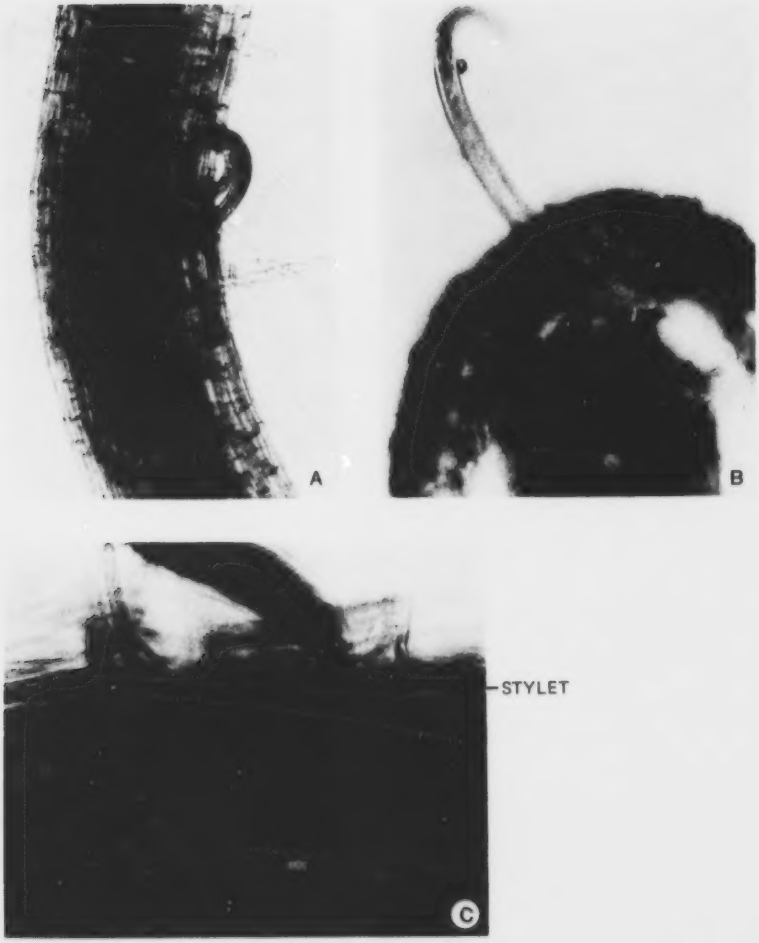


Fig. 6. *A*, *B*, *C*, Some ectoparasites, such as this spiral nematode, *Helicotylenchus digonicus* (Hoplolaimidae), feed with only the anterior end embedded in a root. Note in *C* that the stylet is extended and has penetrated a root cell. Other ectoparasites feed externally along the tips and sides of roots, moving often to new feeding sites. Consequently, the eggs of ectoparasitic species are oviposited in the soil.

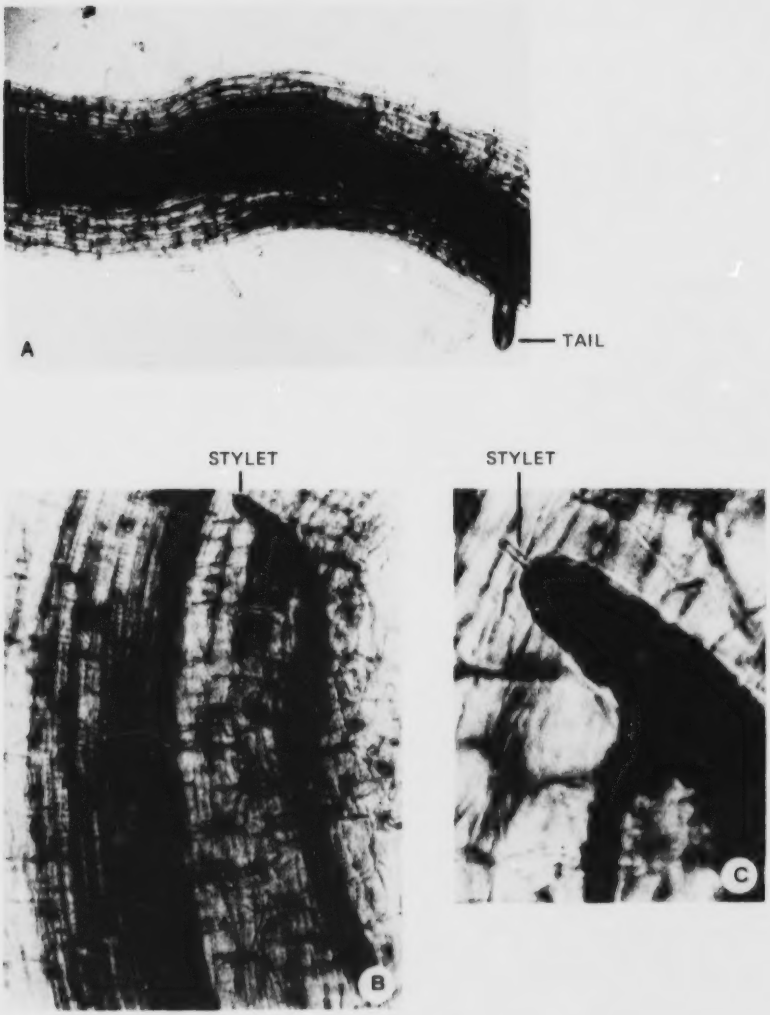


Fig. 7. A migratory endoparasite, such as *Hoplolaimus galeatus* (Hoplolaimidae), penetrates plant roots entirely (*A*) and moves through the cortical tissue, feeding on parenchyma and conducting cells (*B*, *C*). The openings in roots caused by the invasion of nematodes may provide entrances for other parasites and decay organisms.

Fig. 8. The root-lesion nematodes, such as *Pratylenchus penetrans* (Pratylenchidae), are common migratory endoparasites in Canada and attack a wide range of agricultural and garden crops. They are often found in large numbers in root systems (*A*), as well as in the soil. Actively feeding adults lay their eggs within the root tissue (*B*, *C*).

Fig. 9. *A*, En face view of a head comprising 8 sectors, divided by the radial lamina of the head skeleton (*see* Figs. 55, 56). The head of nematodes is typically divided into 6 sectors (Fig. 12*A*). *B* and *C*, Esophageal gland lobes of *Hadrodenus (B)* and *Deladenus (C)* illustrating differences in size and length of the lobes overlapping the intestine. Note the absence of a valvular apparatus in the metacorpus of *Deladenus* in contrast with Fig. 15*A*, *B*.

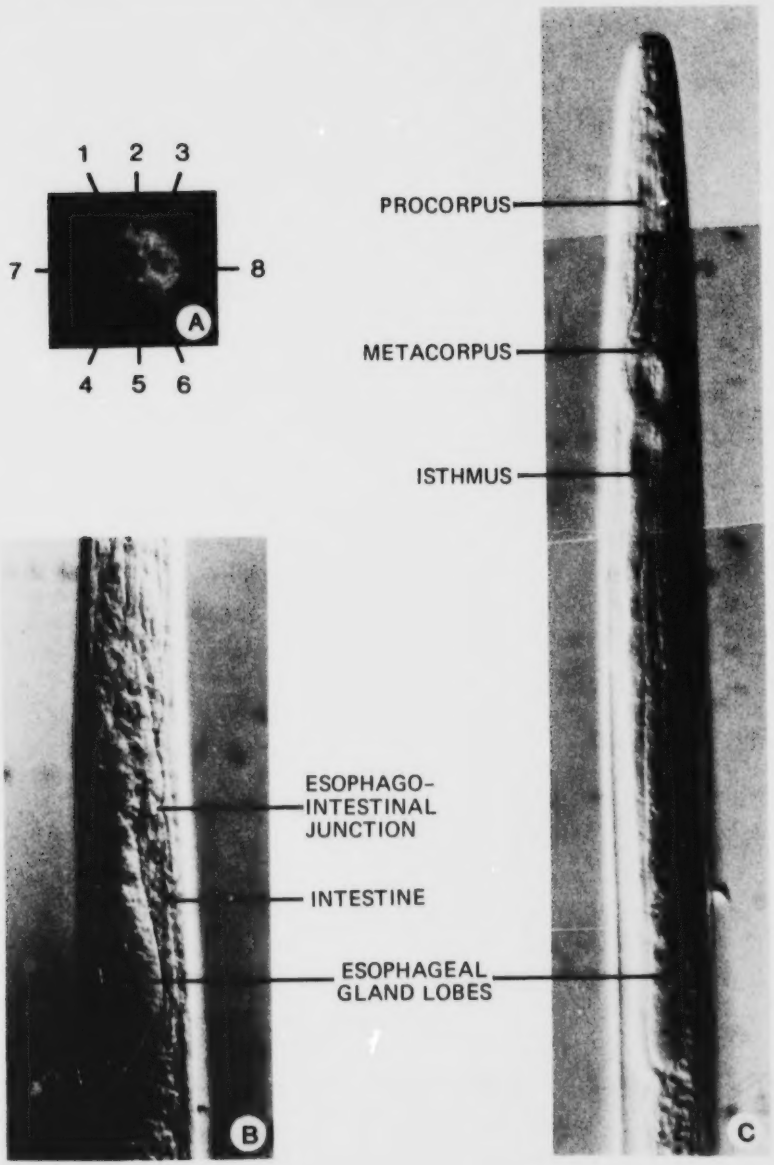

1
2
3
7
8
A
4
5
6
PROCORPUS
METACORPUS
ISTHMUS
ESOPHAGO-
INTESTINAL
JUNCTION
INTESTINE
ESOPHAGEAL
GLAND LOBES
B
C

Fig. 10. *A*, Esophagus of *Hexatylus mulveyi*. This species shows that the esophageal glands, as indicated by one of the gland nuclei (*C*), are not delineated from the intestine in *Hexatylus*. Species of the genus also have prominent intestinal villi (microvilli), which are obscure in most nematodes. *B*, Lateral view of the head end showing the characteristic refractive rings encircling the stylet and the small, bifurcated knobs, as compared with undivided knobs in Fig. 11*A*.

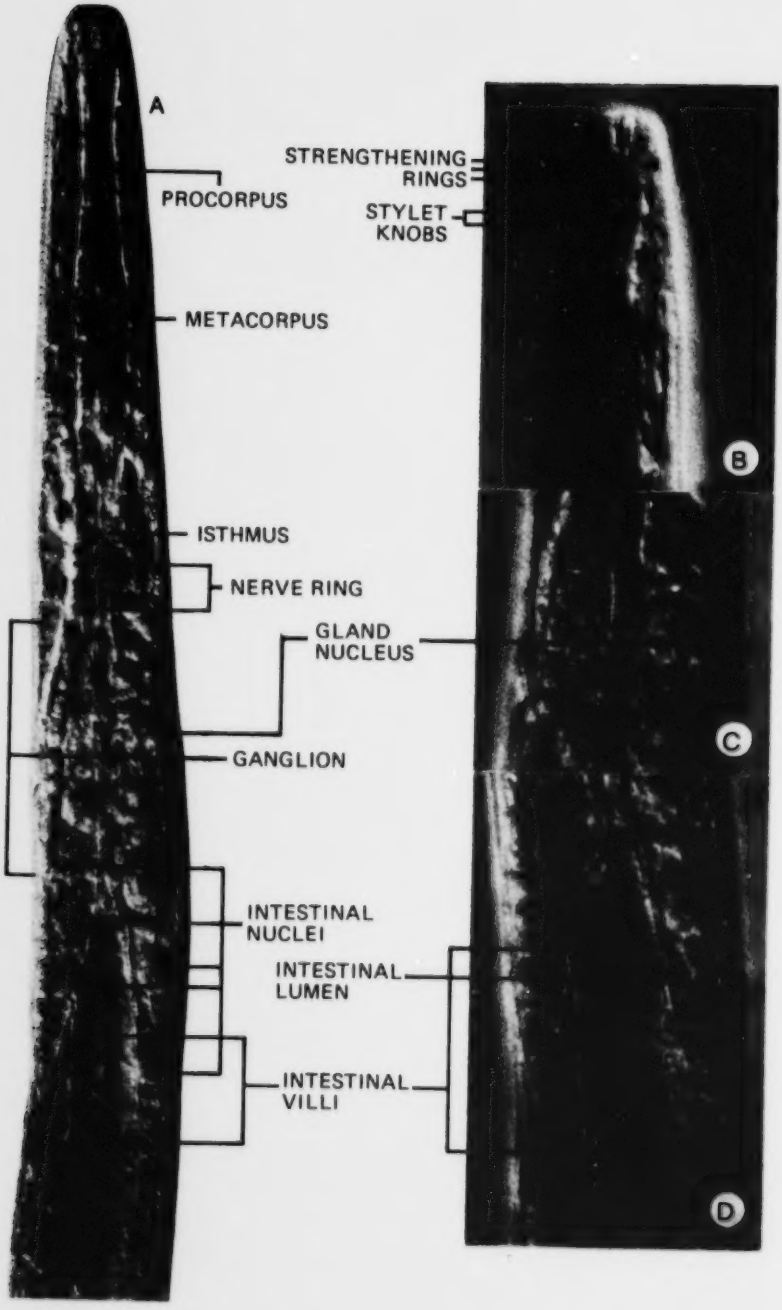

A
PROCORPUS
METACORPUS
ISTHMUS
NERVE RING
GLAND NUCLEUS
GANGLION
INTESTINAL NUCLEI
INTESTINAL LUMEN
INTESTINAL VILLI
STRENGTHENING RINGS
STYLET KNOBS
B
C
D

Fig. 11. *A*, Lateral view of head end and stylet of *Hadrodenus*. *B*, Male tail of *Deladenus*. The bursa encloses the entire tail, which is a diagnostic feature of some species of nematodes, as compared with the bursa in Fig. 14*C*, *D*. *C*, Lateral view of vagina in *Stictylus*. Note the absence of a postuterine branch. *D*, A similar monodelphic, prodelphic species having a rudimentary postuterine branch.

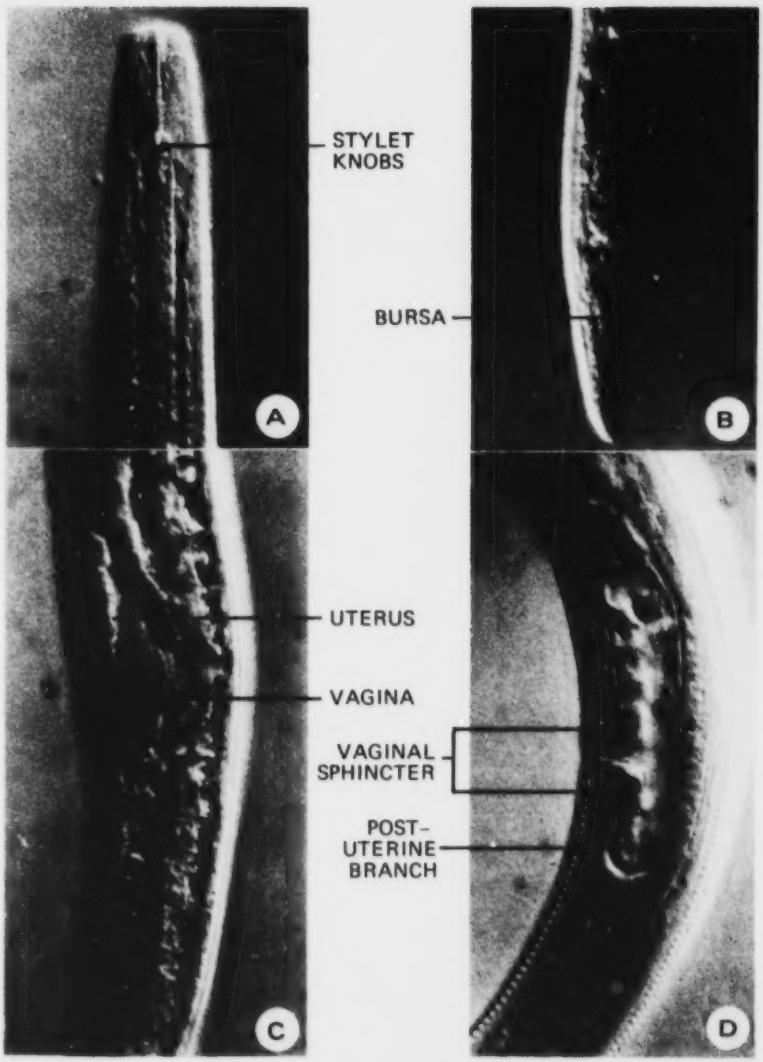

STYLET KNOBS
BURSA
UTERUS
VAGINA
VAGINAL SPHINCTER
POST-UTERINE BRANCH
A
B
C
D

Fig. 12. *A*, En face view of a typical nematode head comprising 6 sectors and divided by the radial lamina of the head skeleton (*see* Figs. 55, 56). *B*, Stylet of *Stictylus* characterized by having knobs at different levels. *C*, Diagnostic form of the esophageal bulb of *Stictylus* having a stem-like projection. *D* and *E*, Other forms of esophageal bulbs are cylindroid (*D*), represented by a species of *Nothotylenchus* and pyriform (*E*), represented by *Boleodorus* sp.

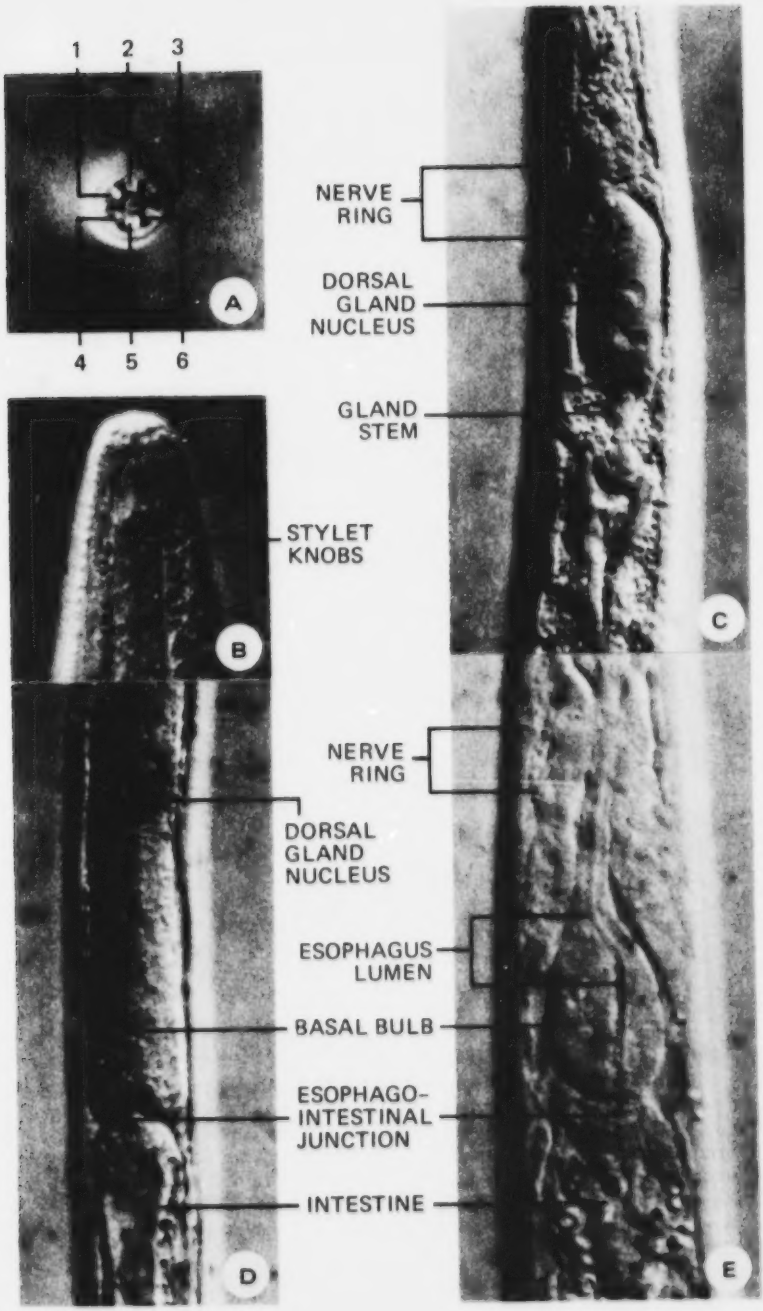
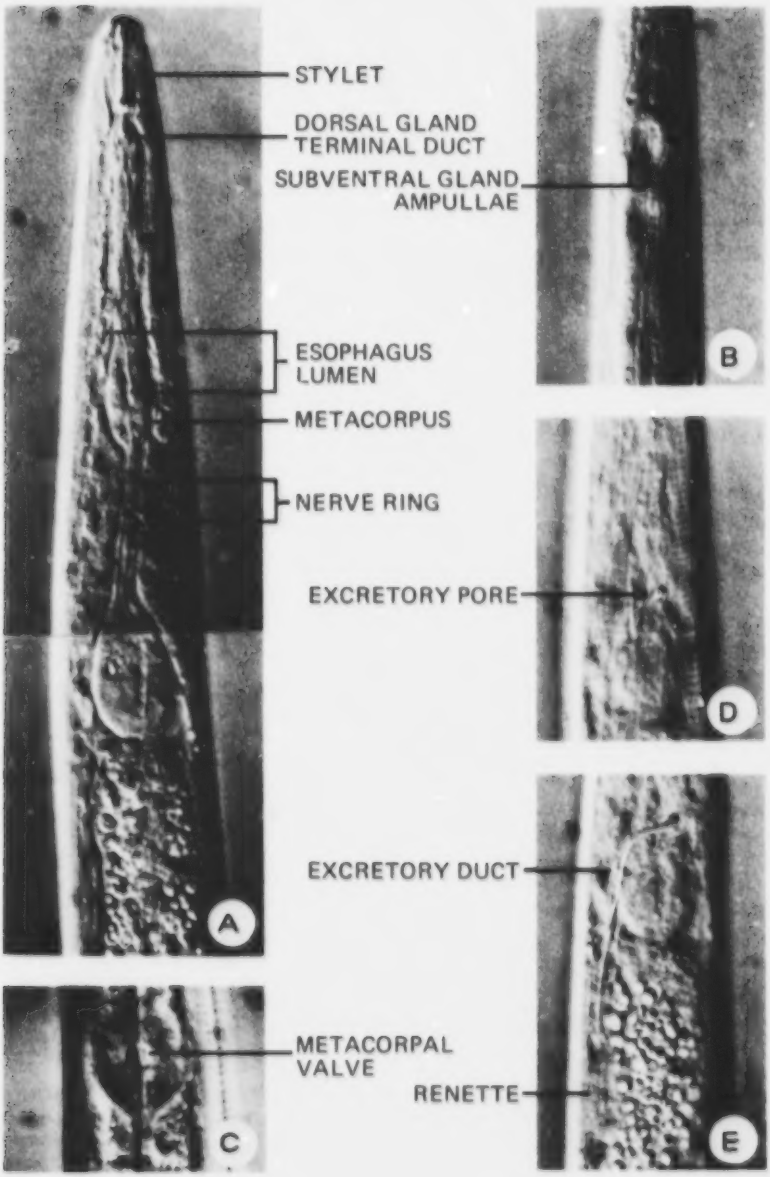

1
2
3
4
5
6
A
B
C
D
E
NERVE RING
DORSAL GLAND NUCLEUS
GLAND STEM
STYLET KNOBS
NERVE RING
DORSAL GLAND NUCLEUS
ESOPHAGUS LUMEN
BASAL BULB
ESOPHAGO-INTESTINAL JUNCTION
INTESTINE

Fig. 13. *A*, Anterior end of *Boleodorus thylactus*, a common terrestrial species in Eastern Canada, showing the stylet and esophagus. *B*, Metacorpal region of a species of *Deladenus*. Note the reduced, fusiform metacorpus and the absence of a valvular apparatus, as in Fig. 10*A*. *C*, A well-developed metacorpus with a valvular apparatus, representative of the Tylenchoidea. *D* and *E*, Except for the Longidoridae, plant-parasitic nematodes have an excretory system with a well-defined external opening or pore and duct, and a usually obscure renette. Differences in position of the pore and in cuticularization (refractiveness) of the excretory duct are useful identification aids.


STYLET
DORSAL GLAND TERMINAL DUCT
SUBVENTRAL GLAND AMPULLAE
ESOPHAGUS LUMEN
METACORPUS
NERVE RING
EXCRETORY PORE
EXCRETORY DUCT
METACORPAL VALVE
RENETTE
A
B
C
D
E

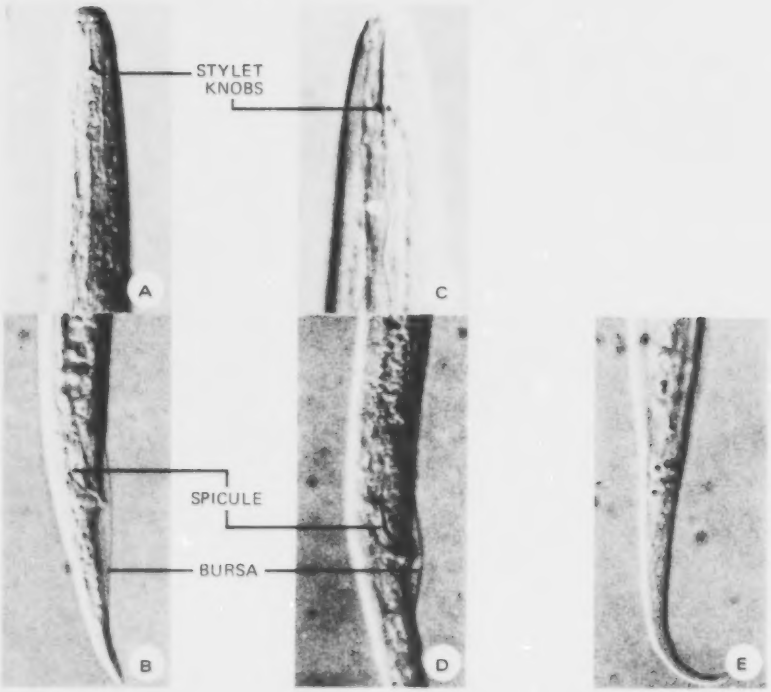


Fig. 14. Head and stylet shape (*A*) and male tail (*C*) characteristic of species of *Nothotylenchus*. Note the rounded stylet knobs and size of the bursa in relation to length of the tail. These species are similar to and may be confused with *Ditylenchus* (Tylenchidae). By contrast, species of *Boleodorus* have a stylet with "flanged" knobs (*C*); the male tail has a short, adanal bursa (*D*); and the female tail often is hooked at the end (*E*).

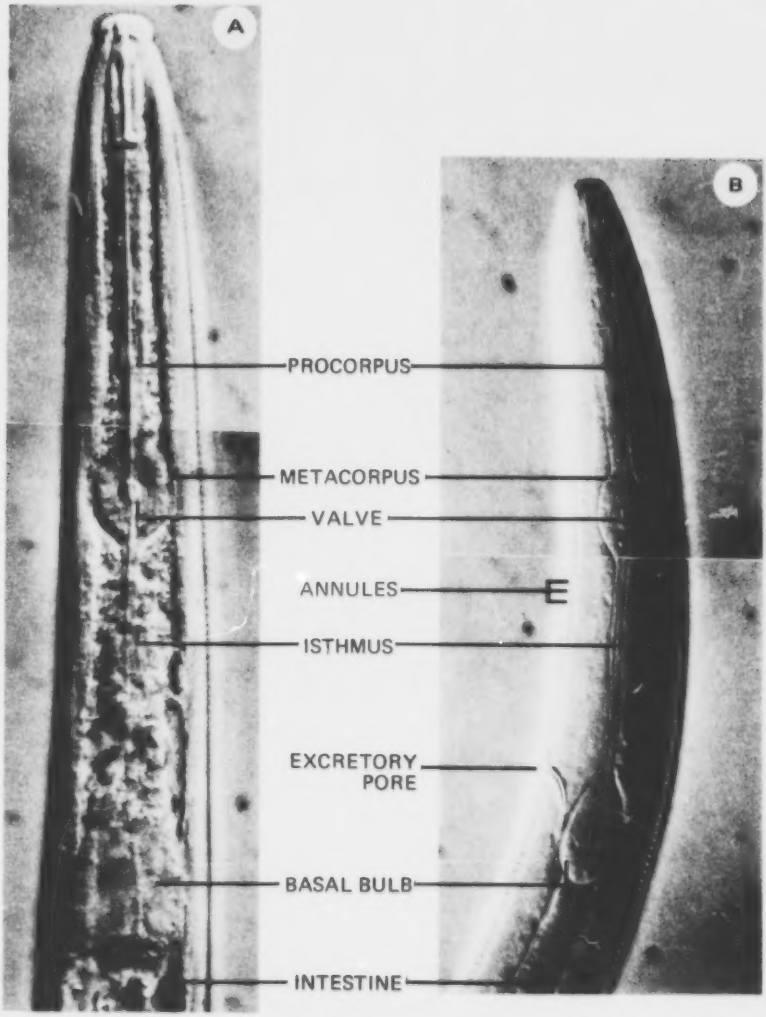


Fig. 15. Examples of common Canadian species having esophageal glands contained in a bulb that does not overlap the intestine but is apposed. Note also the differences in size of the body annules, which are typical for many of the plant-parasitic nematodes. *A*, Esophagus of *Tylenchorhynchus dubius* (Tylenchorhynchidae). *B*, Esophagus of *Tylenchus davainei* (Tylenchidae).

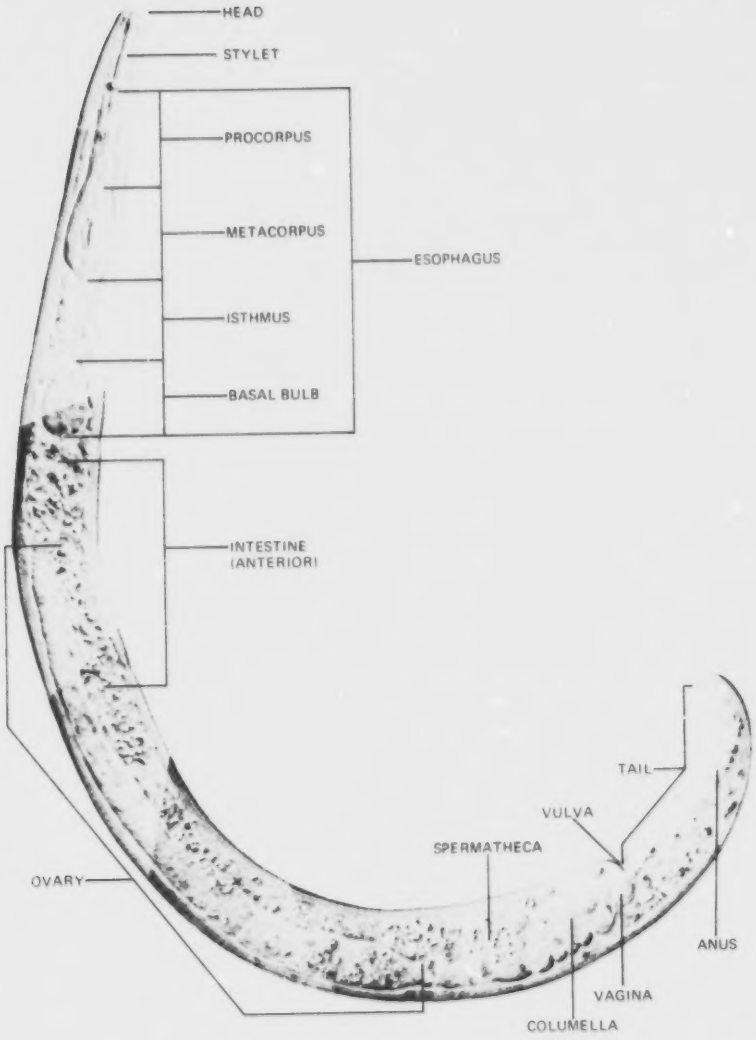


Fig. 16. Adult female of *Paratylenchus*, a pin nematode, showing the parts of the body that are of particular diagnostic importance. The posteriorly expanded procorpus and the large metacorpus, which contains a massive valvular apparatus, as compared with Figs. 2 and 15, are the most important diagnostic features of the superfamily Criconematoidea. All species also have one ovary (monodelphic) that is directed anteriorly (prodelphic). Because the anus is often obscure, the distance between the vulva and tail tip is usually considered as the tail.

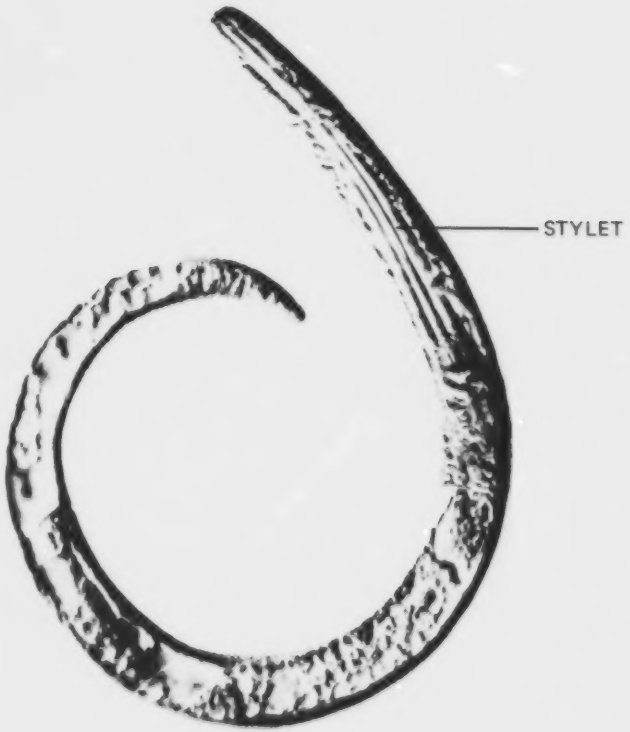


Fig. 17. Adult female of *Gracilacus aciculus*. Members of this genus are very small, usually less than 400 μm long, and typically have elongated, conoid tails (Fig. 19*A*). Note the great length of the stylet in relation to body length as compared with *Paratylenchus* (*see* Fig. 16).

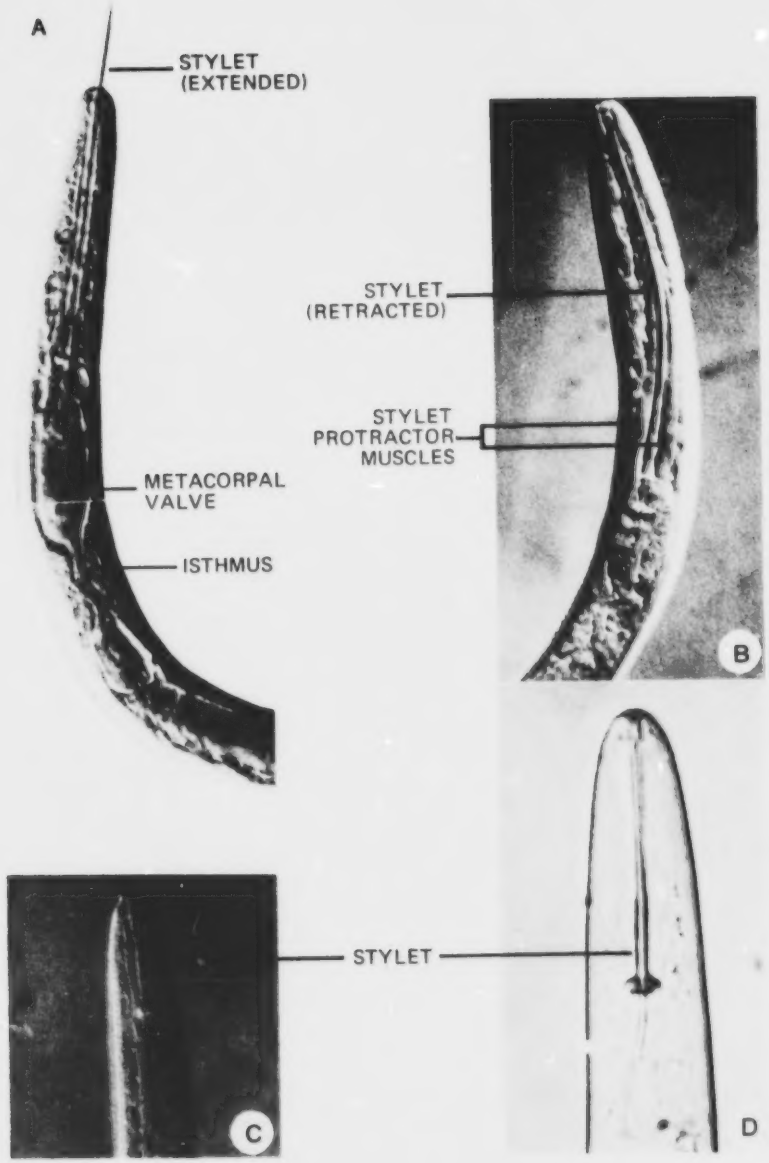


Fig. 18. *A* and *B*, *Gracilacus aculentus*. Anterior ends of adult females with stylet extended for feeding (*A*) and retracted (*B*). When retracted, the stylet base is in the metacorpus. *C* and *D*, Two species of *Paratylenchus* showing diagnostic differences in head shape and stylet length. Note the straight, rigid form of the retracted stylet compared with the longer, more flexible stylet in *Gracilacus* (*B*).

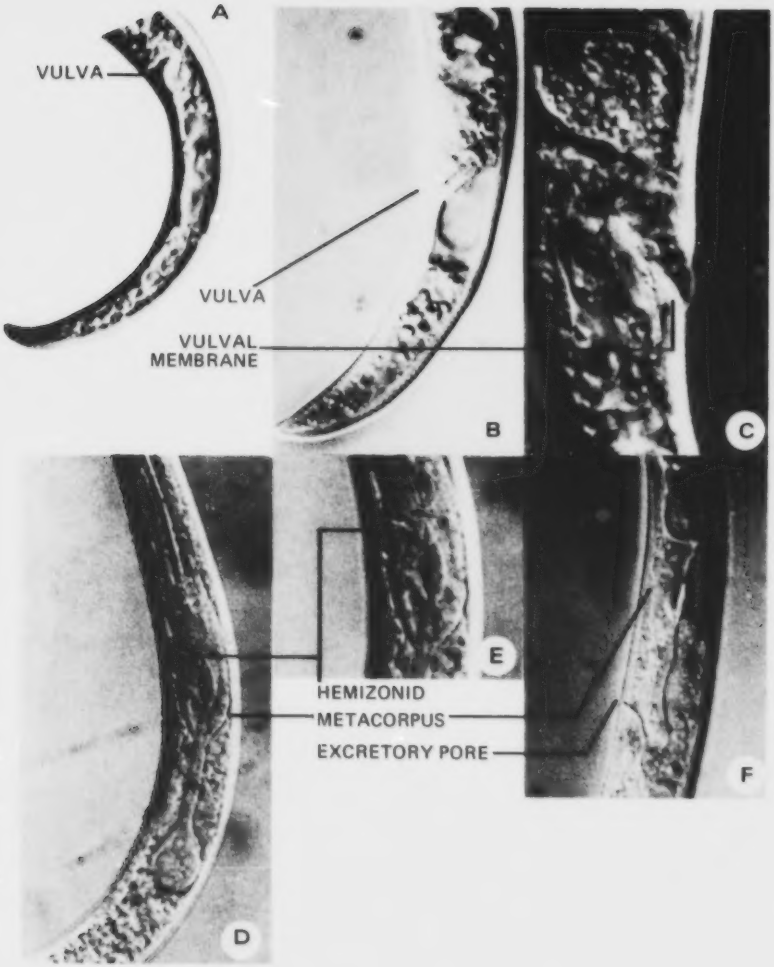


Fig. 19. *A* and *B*, Examples of typical differences in length and taper of the tail (vulva to tail tip) in species of *Gracilacus* (*A*) and *Paratylenchus* (*B*). *C*, Presence of a vulval membrane is a characteristic feature of *Paratylenchus* spp. *D* and *E*, Esophageal region of *Gracilacus* showing the position of the hemizonid and excretory duct (not visible) in relation to the metacorpus. *F*, Esophageal region of *Paratylenchus*. The hemizonid (not visible) and excretory pore in species of this genus are posterior to the metacorpus. In species of the order Tylenchida, the hemizonid is in close proximity to the excretory pore, usually immediately anterior.

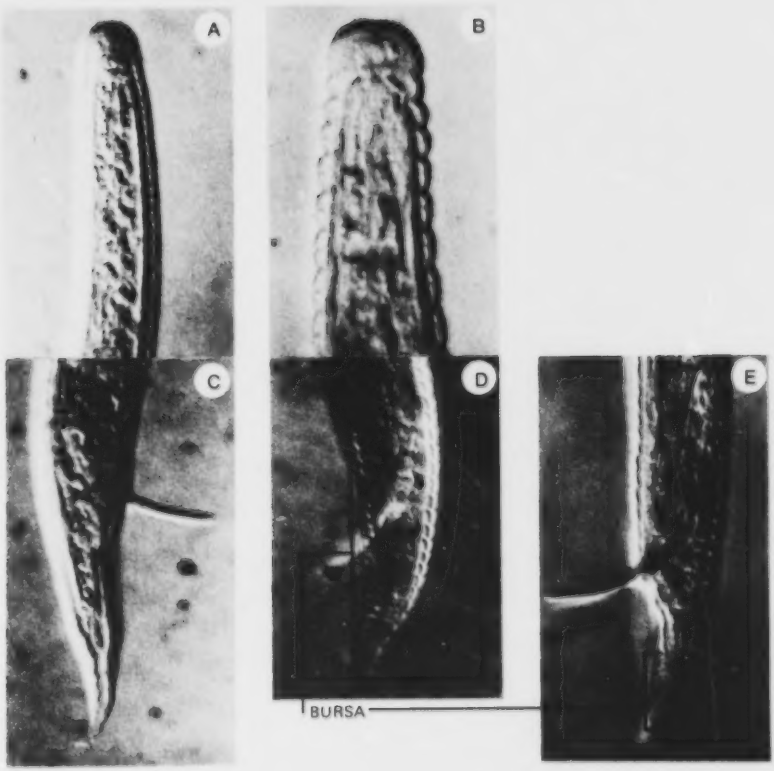


Fig. 20. Males of the pin nematode (Paratylenchidae) and ring nematodes (Criconematidae) are degenerate, having a weakly developed esophagus and frequently lacking a stylet (*A, B*). A species may lack a bursa (*C*) or have a well-developed (*D*) or reduced (*E*) bursa. The presence or absence of males in a given species is of supplementary diagnostic value.

Fig. 20.5. Adult female of *Nothocrinconema petasum*. The large body annules immediately identify this species of plant-parasitic nematodes as a ring nematode (Criconematidae). Such species, when observed in a water suspension or on a slide mount, often have soil particles and debris lodged between the annules. Note that the posterior second head annuled of this species is markedly reduced.

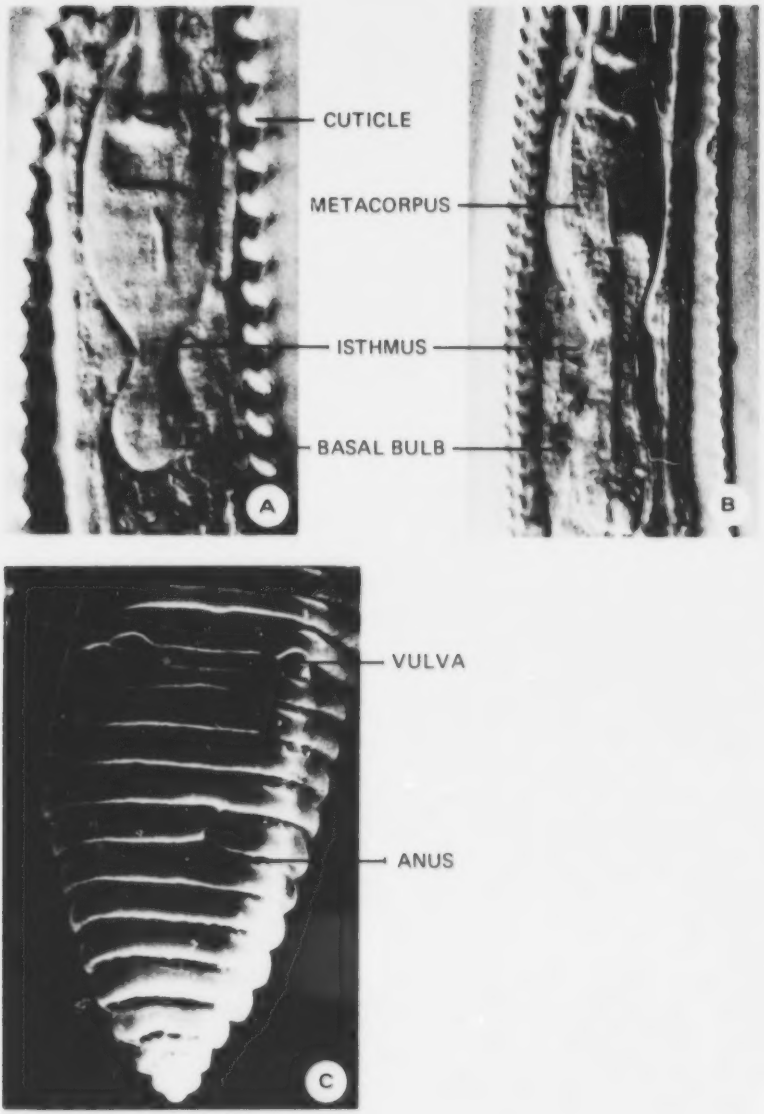


Fig. 21. *A* and *B*, Esophagi of two species of Criconematidae illustrating the diagnostic features representative of this family. Note the short isthmus and reduced basal bulb as compared with their close relatives in the Paratylenchidae (*see* Figs. 16, 18*A*). *C*, Scanning micrograph of the posterior, ventral surface of an adult female criconematid (ring nematode) showing the vulval shape and the typically small anus, which is often obscure at the lower magnifications of the light microscope.

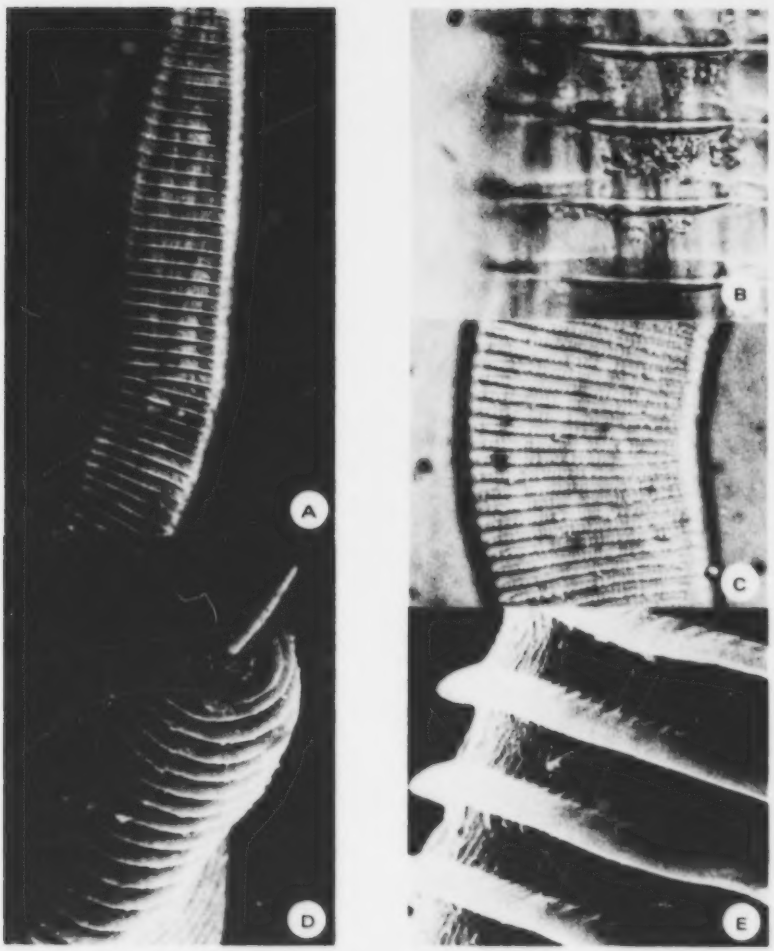


Fig. 22. *A*, *B*, and *C*, Examples of body annule form in those species of ring nematodes having smooth (*A*), irregular (*B*), and crenate (*C*) margins. *D*, Scanning micrograph of the head of a smoothly annulated species with a protruding stylet. *E*, Scanning micrograph enlargement of the body annules of the same species.

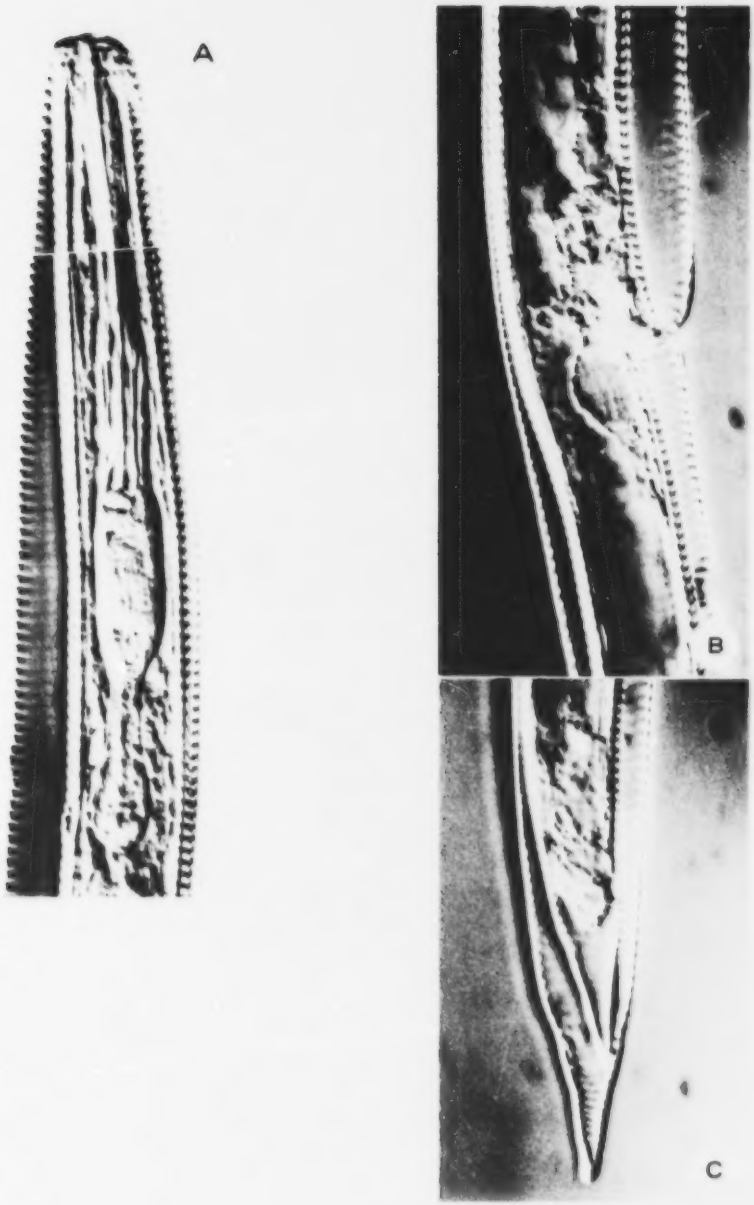


Fig. 23. *Hemicycliophora*, the sheath nematode. *A*, Anterior end of female. *B*, Vulval region. *C*, Tail. Adults of this genus retain the final molting cuticle, which is a unique feature in nematodes.

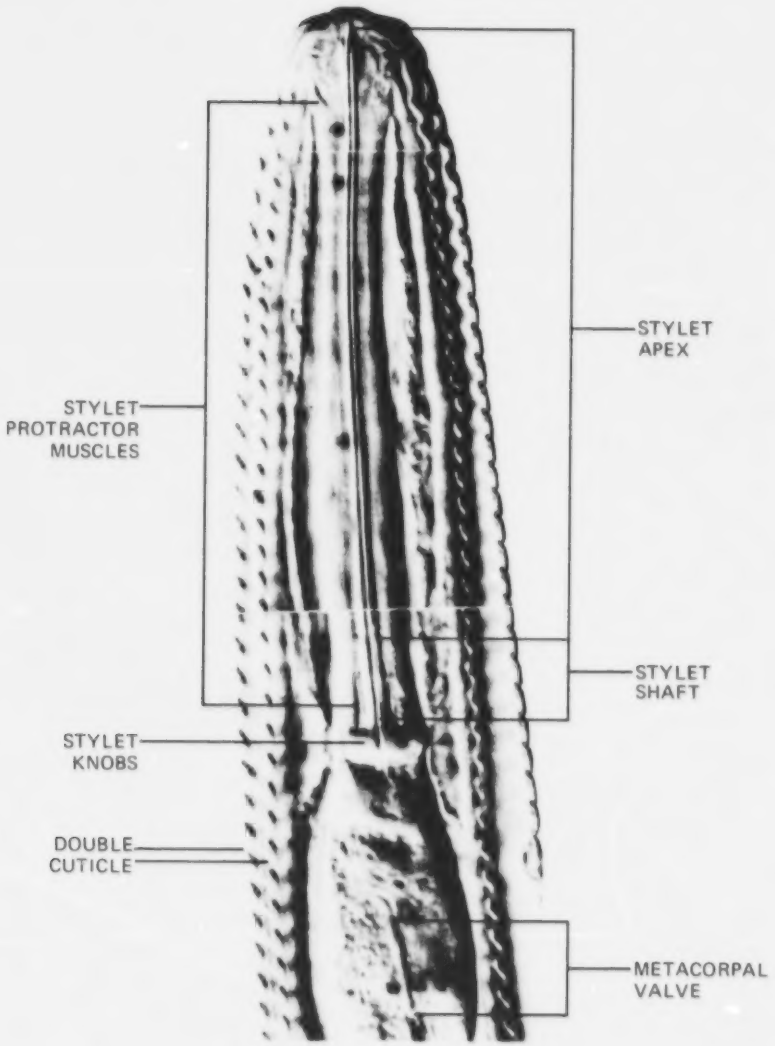


Fig. 24. Head end of an adult *Hemicycliophora shepherdi*. Note the long stylet apex in relation to the short shaft, which is a characteristic of the Criconematoidea (*compare with* Fig. 56*E*). The strong stylet protractor muscles that attach to the knobs and, anteriorly, to the sides of the head between the somatic muscles are also conspicuous. The double cuticle immediately separates this species from those of all other genera occurring in Canada.

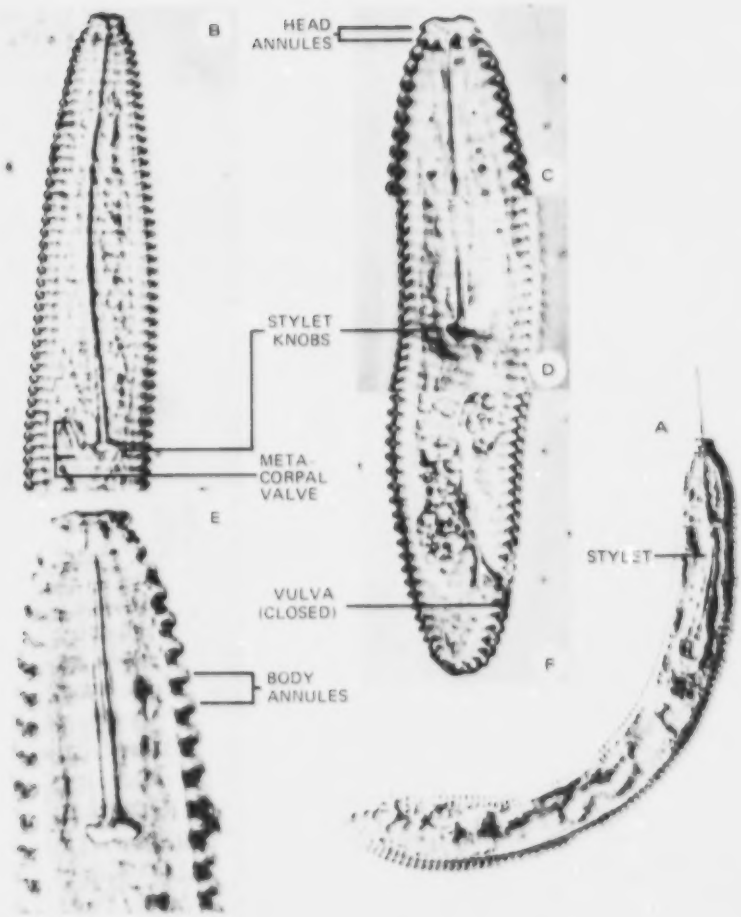


Fig. 25. *A*, *B*, *C*, *D*, and *E*, *Xenocriconemella macrodora*. *A*, Adult female. Note the great length of the flexible stylet in relation to body length, the coarseness of body annulation, and the shape of the short, hemispherical tail (vulva to tail tip). *B*, Anterior end showing the retracted stylet with the base deeply embedded in the metacorpus, which is a characteristic feature of many ring nematodes. *C*, Enlargement of the head showing the form and head annules, which are undifferentiated in contrast with Figs. 20.5; 27*A*, *B*; 31*A*. *D*, Stylet knobs. *E*, For contrast, a more typical species of other criconematid genera having a short, rigid stylet (*see also* Figs. 1, 28*A*). *F*, Example of a species having a closed vulva. An example of an open vulva is shown in Fig. 27*D*.

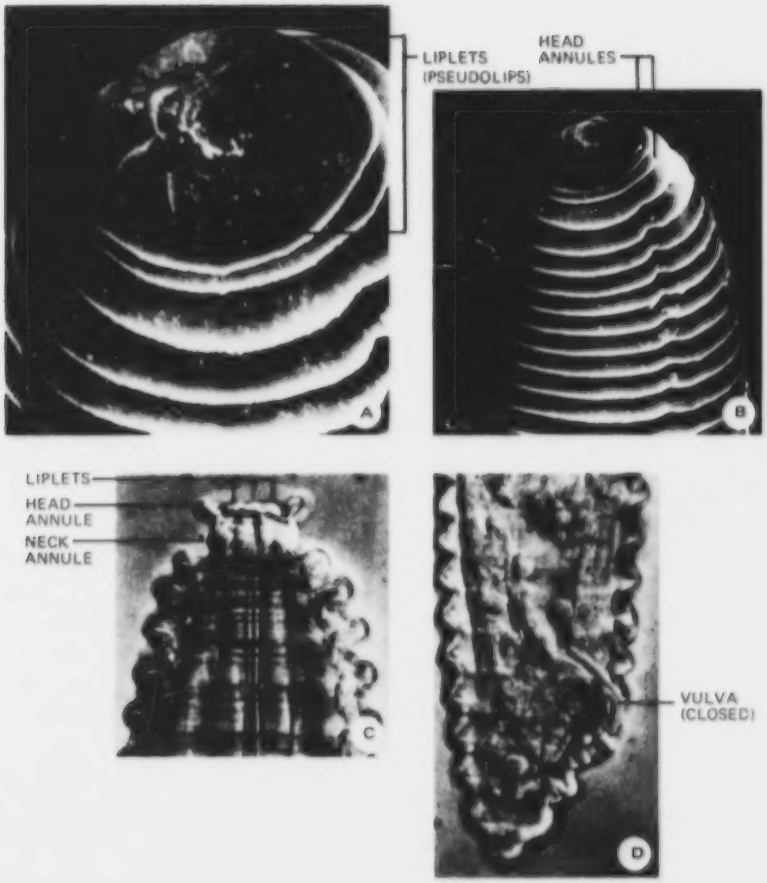


Fig. 26. *A*, Scanning micrograph enlargement of the head apex characteristic of species of *Northocriconema*, which have 6 reduced lips or liplets (pseudolips). *B*, Scanning micrograph of the same species at a lower magnification, illustrating the number and shape of the head annules compared with body annules. *C*, Lateral view of the head of another species of *Nothocrinconema*. Note that this species has a single enlarged head annule, followed by a narrow collar (neck) bearing a small neck annule. *D*, Posterior end of a species having a closed vulva and conoid tail.

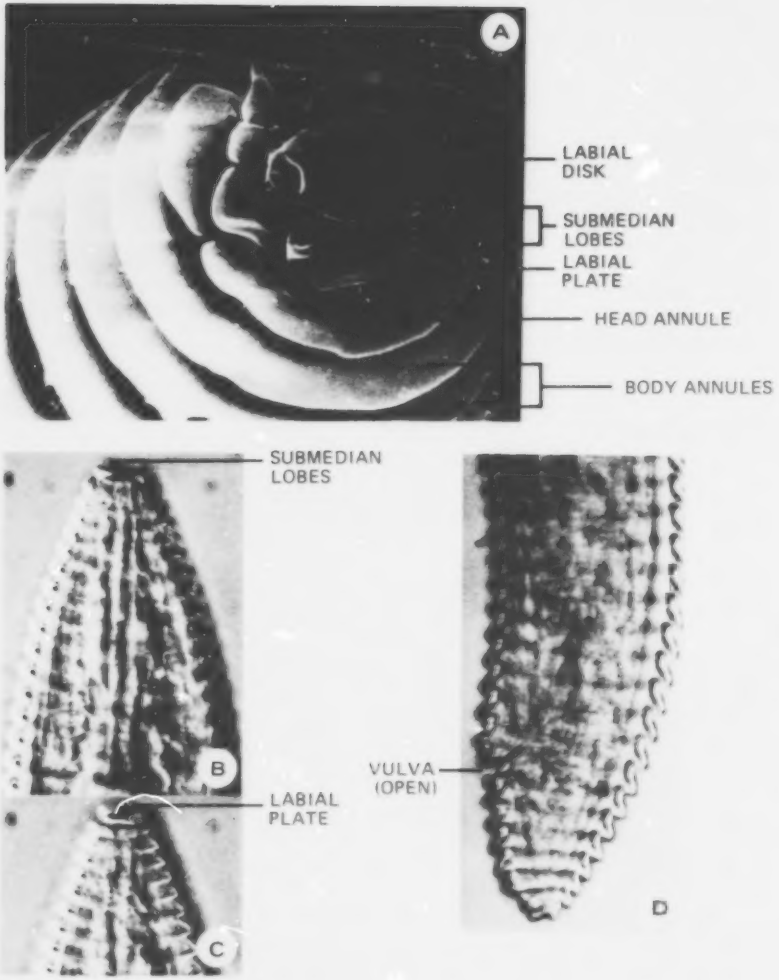


Fig. 27. *A*, Scanning micrograph of the head of a species of *Macroposthonia* characterized by having the typical 6 lips reduced to 4 submedian lobes, as compared with the 6 reduced lips shown in Fig. 26*A*. The 1st and sometimes 2nd head annule are typically divided, forming a circlet of labial plates. *B*, Lateral view of *M. rustica* having large, flattened submedian lobes. *C*, Lateral view at outer contour of head showing a single labial plate. *D*, Species in this genus generally have an open vulva as shown.

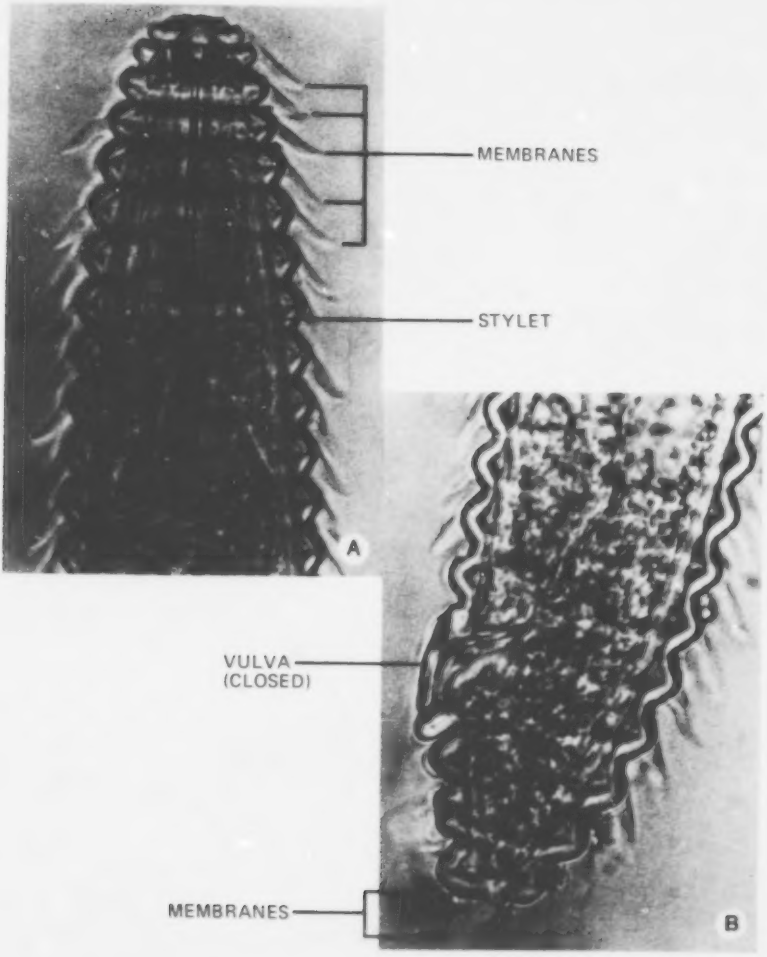


Fig. 28. *Bakernema*. *A*, Anterior end of a preserved adult female. *B*, Tail of adult female showing membranes. Note that the closed vulva is covered by a long flap of cuticle. Species in this genus have long, transparent membranes on the body annules. These diagnostic structures are conspicuous in living specimens, but tend to become obscure or disappear when the specimens are killed by heat and preserved.

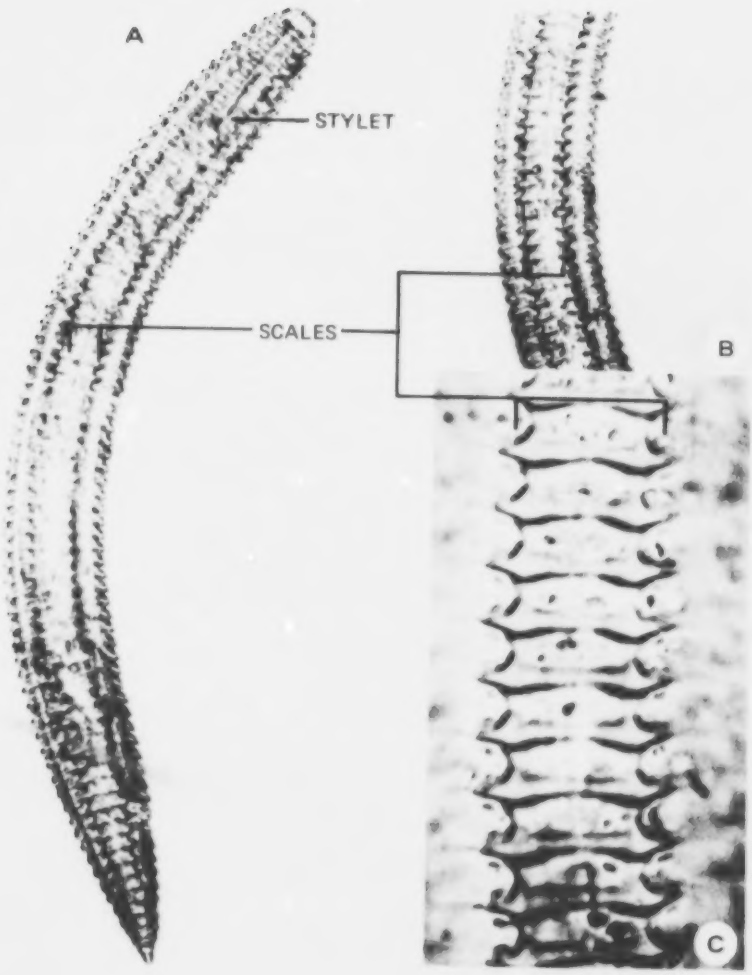


Fig. 29. *A*, Adult female of a species of *Criconema*. The coarse body annules of species in this genus are characterized by longitudinal rows of thickenings, called scales. *B* and *C*, Surface views of the body annules illustrating the form of the scales at the inner margins between 2 longitudinal rows.

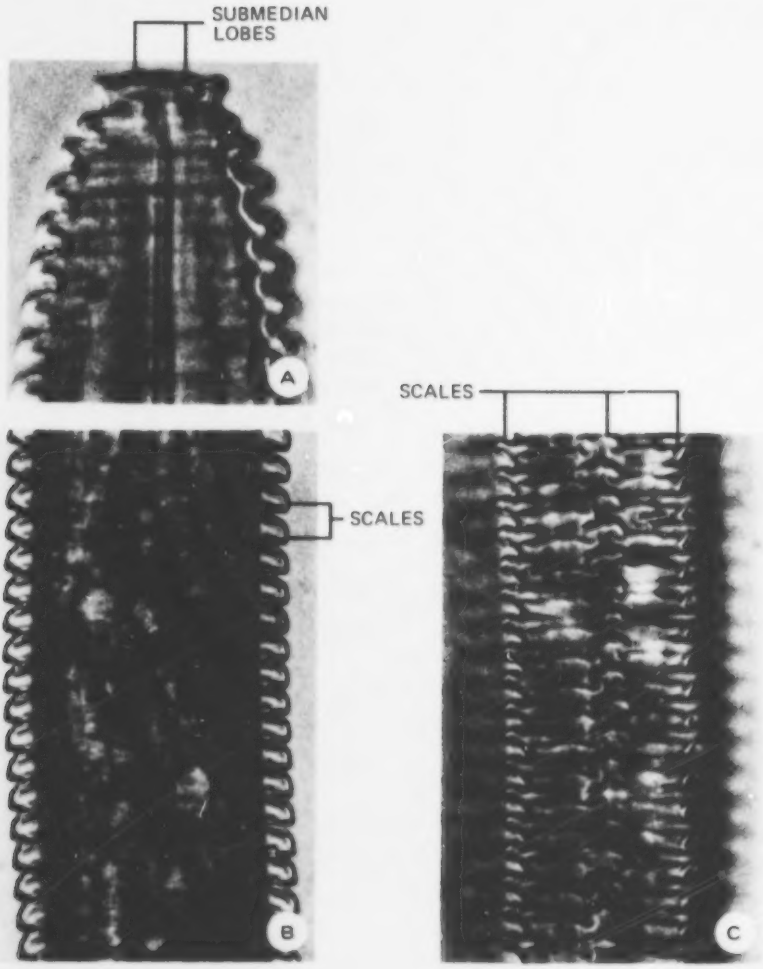


Fig. 30. *Criconema octangulare*. *A*, Lateral view of head bearing the characteristic submedian lobes rather than liplets. *B*, Lateral view through scales near midbody. *C*, Surface view showing the form of scales from a top view of a single longitudinal row.

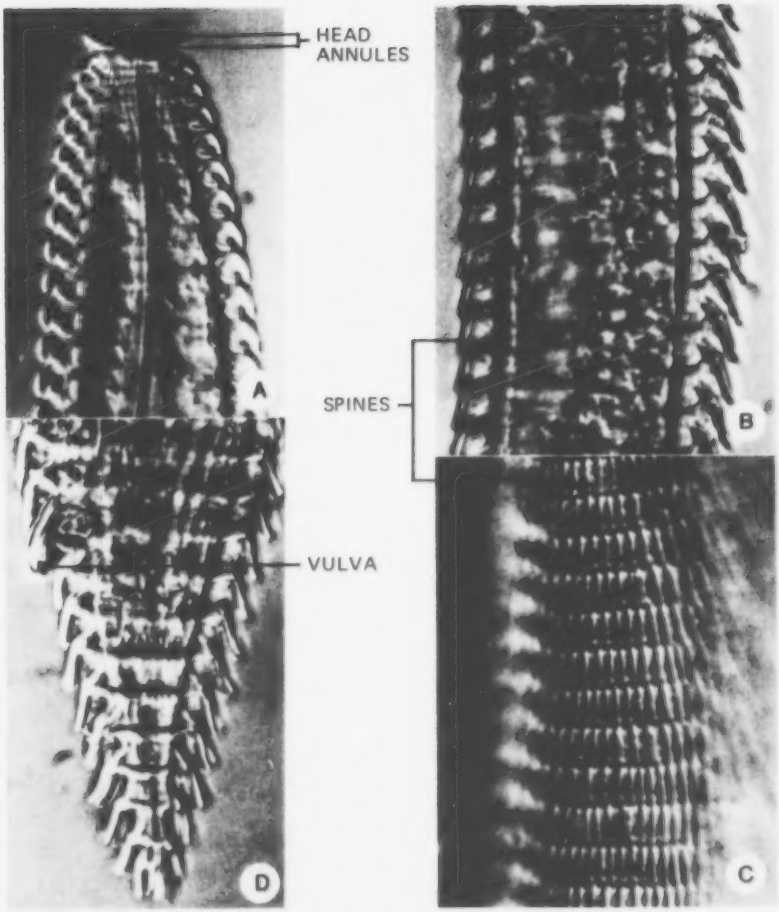


Fig. 31. *Crossonema menzeli*. *A*, Lateral view of head end. Note the asymmetry of the head annules and the dome-shaped head apex. Species of this genus have long, retrorse spines on the body annules. *B*, Lateral view at midbody through the spines. *C*, Surface view of spines. In some species the spines are arranged in a continuous series rather than in longitudinal rows (*see* Fig. 32). *D*, Tail end illustrating a closed vulva covered by a large cuticular flap (*compared with* Fig. 26*D*).

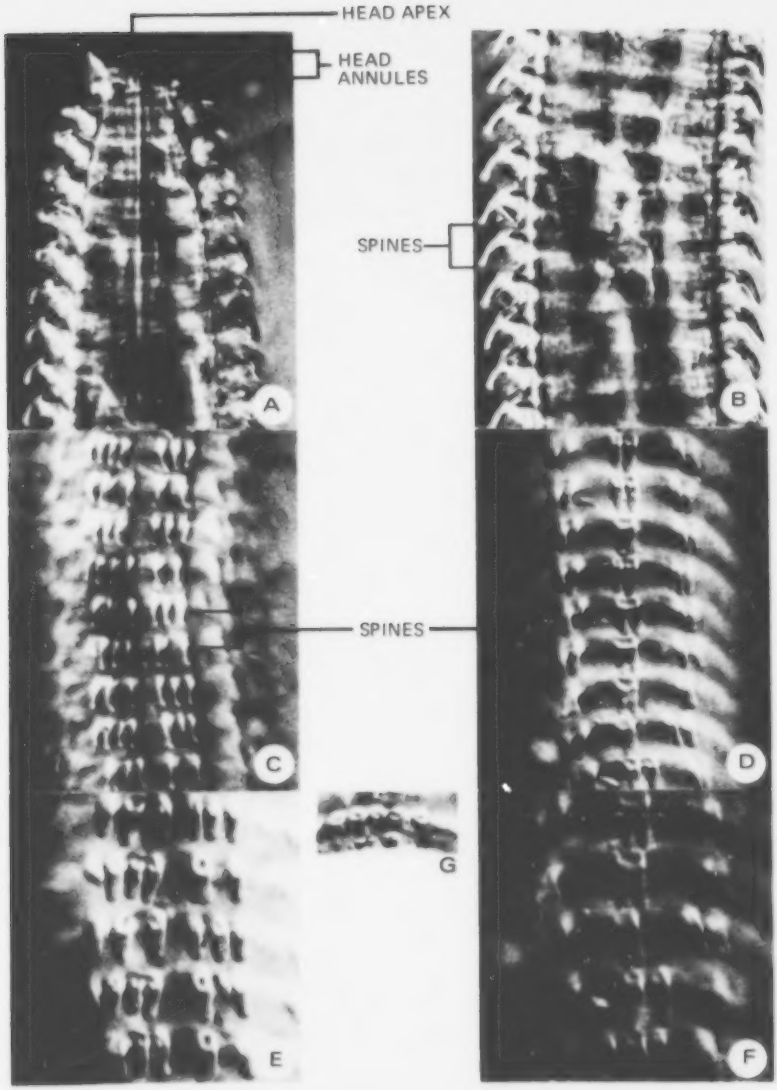


Fig. 32. *Crossonema seymouri*. *A*, Anterior end. Note the differences in shape of the labial annules and the more flattened head apex as compared with Fig. 31*A*. *B*, Lateral view near midbody through the spines. *C*, *D*, *E*, and *F*, Surface views of spines. In some species the spines are arranged in groupings of 1 to 4 in longitudinal rows. *G*, View of spines at junction with the body annule showing their hollow structure.

Fig. 33. Adult females of *Tylenchus* (*A*) and *Cephalenchus* (*B*) showing typical body proportions of members of the family Tylenchidae. Many of these species have tails that are elongate-conoid (*A*) to filiform (*B*). The length of the tail is often expressed as a ratio of the distance between the vulva and anus. Representatives of the Tylenchidae are common in species mixtures extracted from soil samples.

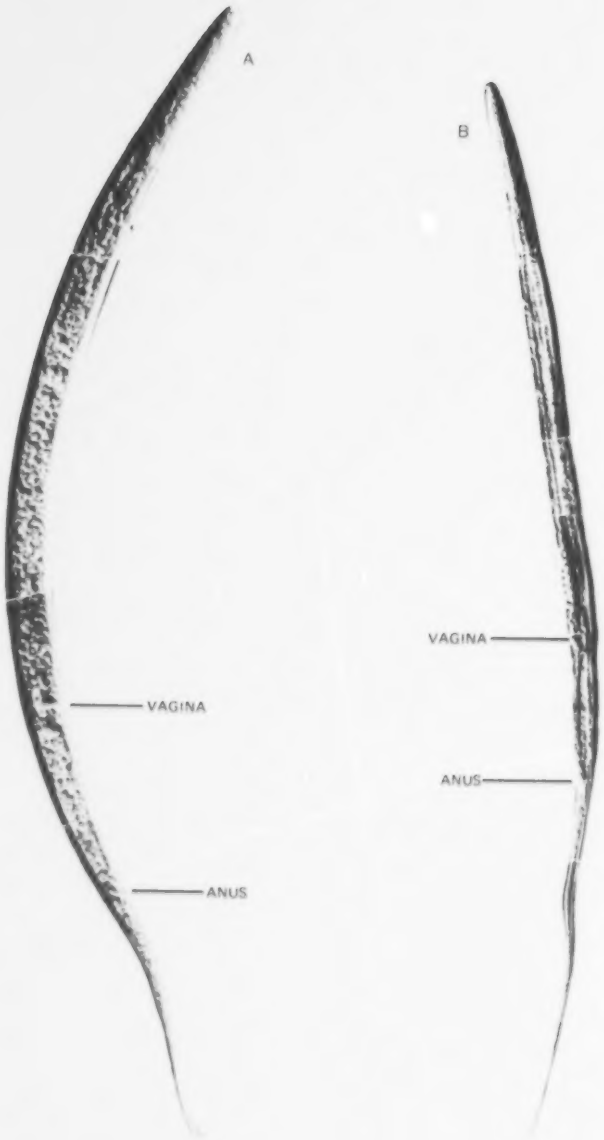
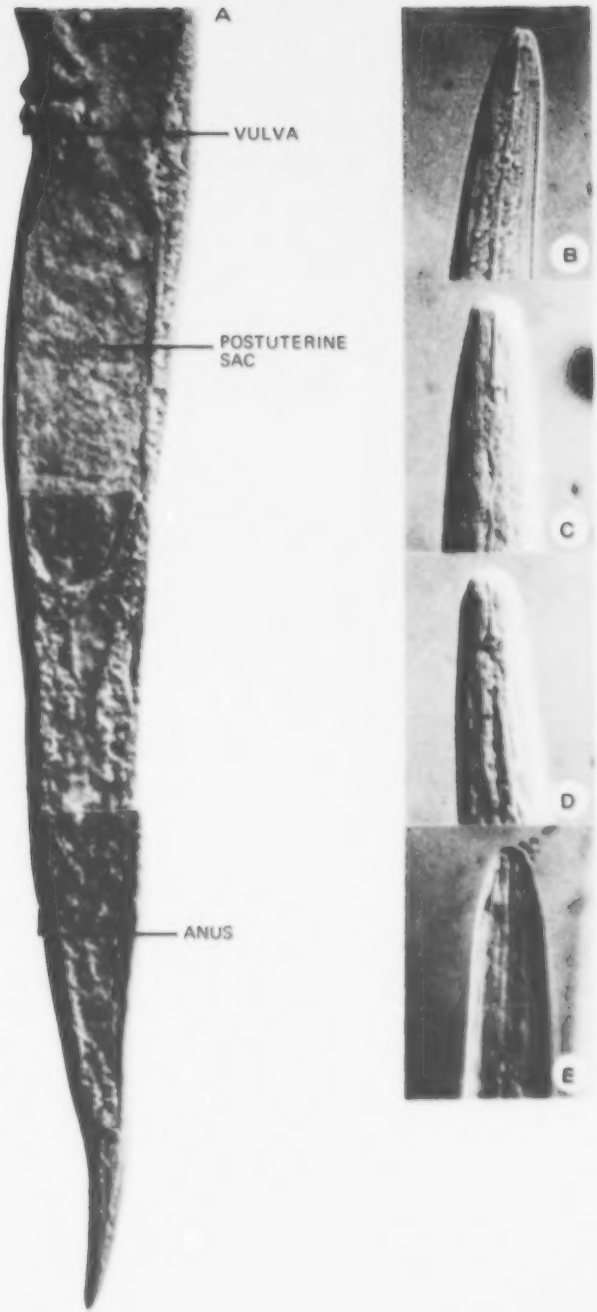

A
VAGINA
ANUS
B
VAGINA
ANUS

Fig. 34. *A*, Posterior end of *Ditylenchus destructor*, the potato-rot nematode. Species of this genus, in contrast with Fig. 33 *A* and *B*, generally have a short, conoid tail that is less than half the vulva-to-anus length. *B* and *C*, Heads of two *Tylenchus* species. The head skeleton of these species is typically obscure and the lips tend to be annulated as in *C*. *D*, Head of *Ditylenchus* sp. Species of this genus usually have a more refractive, yet weakly developed head skeleton and the lips are not annulated. *E*, Example of a Tylenchidae species having a stylet that lacks knobs. In *B*, *C*, *D*, and *E*, note the relatively weak development of the head skeleton and small proportions of the stylet as compared to the more robust species shown in Figs. 46, 47, 53, and 56.


A
VULVA
POSTUTERINE SAC
ANUS
B
C
D
E

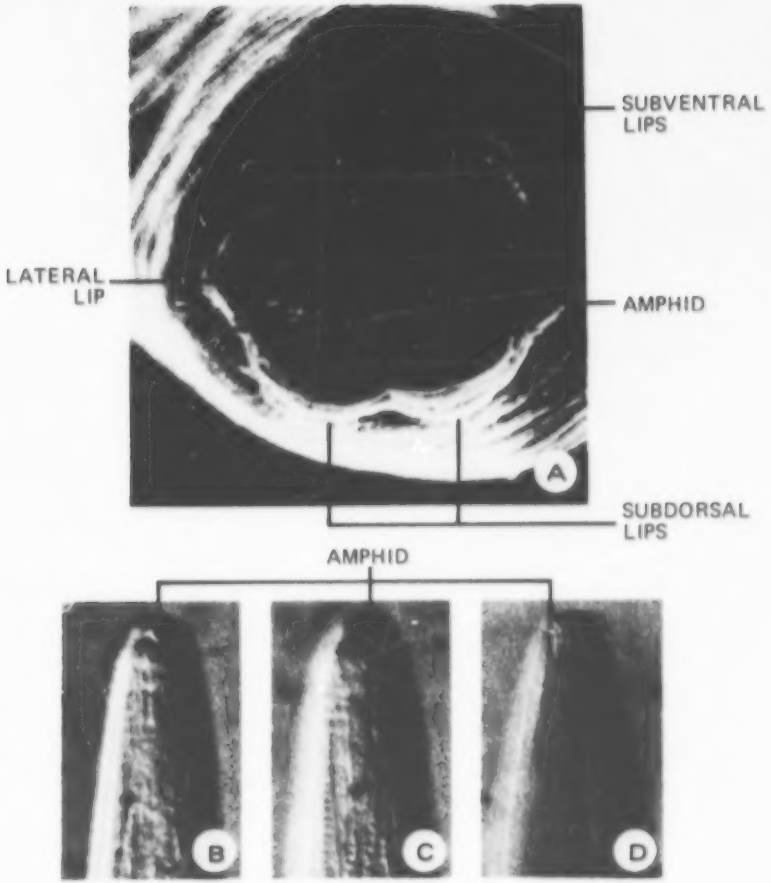


Fig. 35. *A*, Scanning micrograph of the head of *Anguina* sp., one of the seed gall nematodes. As is common to many nematodes the head has 6 uniform lips and the small, oval amphid apertures are near the oral opening (perioral) (*see also* Figs. 53*A*, 65*C*, 67*A*). *B*, *C*, and *D*, *Neopsilenchus* sp. Some species of the subfamily Psilenchinae have elongated amphid apertures that are located on the sides of the lips, as illustrated in a subventral view (*B*), ventral view (*C*), and lateral view (*D*) of the head. This conspicuous characteristic immediately distinguishes these species, some of which are common in Canadian soils, from all other plant-parasitic nematodes.

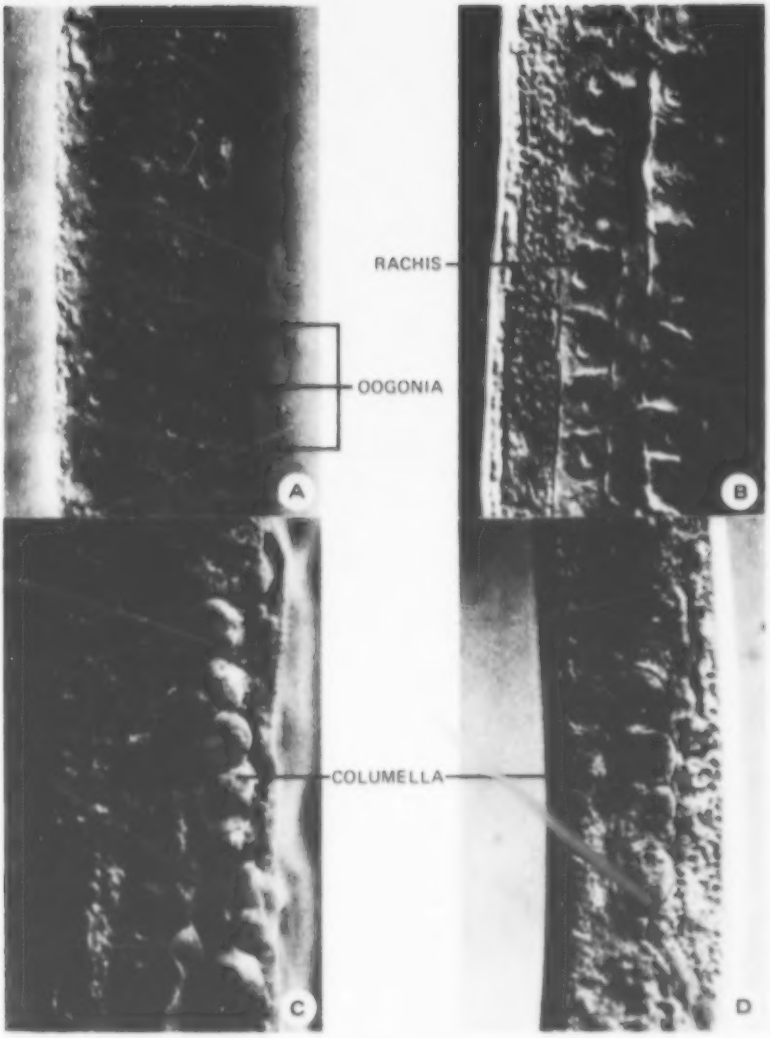


Fig. 36. *A*, Surface view of the ovary in *Anguina* sp., a seed gall nematode. Note that the germinal cells (oogonia and oocytes) are arranged in multiple rows. *B*, Longitudinal section through the centre of the ovary showing arrangement of the germinal cells around a rachis or central core. *C*, *Anguina* sp. An asymmetrical columella composed of cells that are not organized in regular columns. *D*, *Ditylenchus* sp. A symmetrical columella showing 2 of the 4 columns containing 4 cells each. This arrangement is termed a quadricolumella.

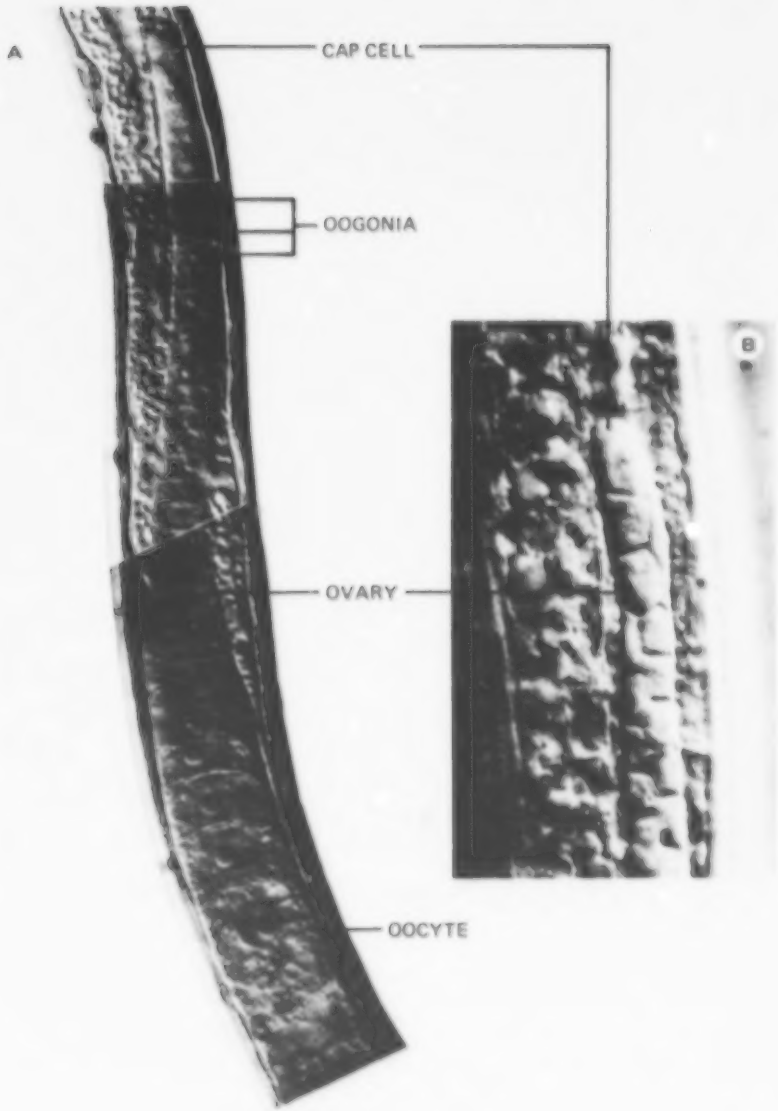


Fig. 37. Examples of ovaries common to most plant-parasitic species. *A*, Ovary with germinal cells arranged in tandem. *B*, Ovary with germinal cells organized in a double row, which is common in the ovarial zone of proliferation.

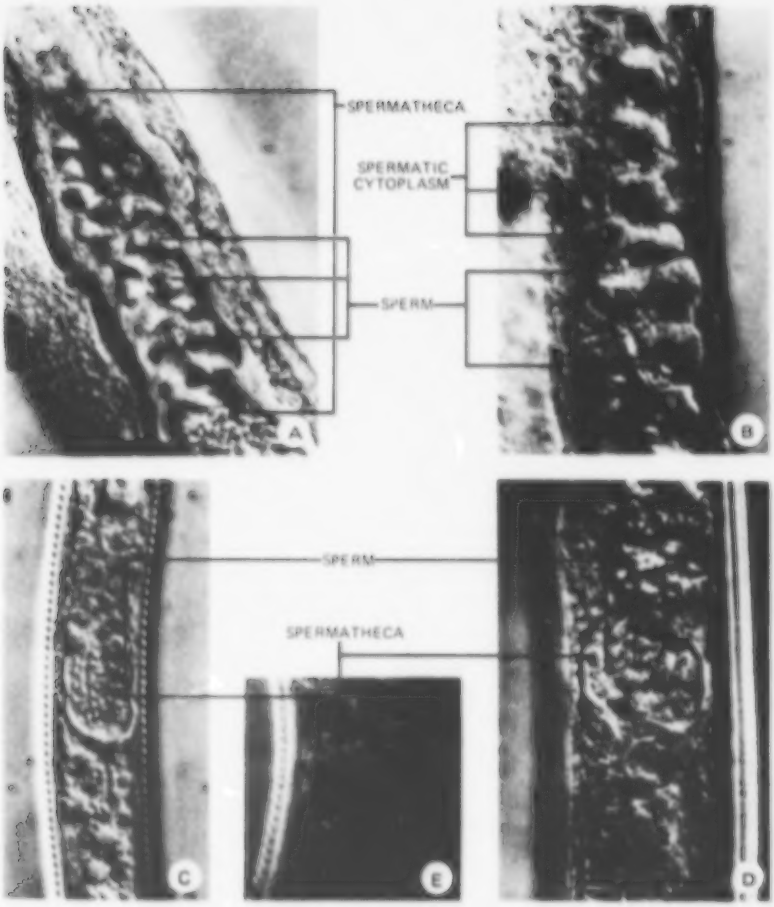


Fig. 38. *A* and *B*. Tubular-shaped functional spermatheca containing sperm (spermatozoa) that are enclosed within cytoplasm that has a membrane-delineated covering. *C* and *D*, Spherical, functional spermathecae containing sperm that have little or no visible cytoplasmic covering. *E*, An empty, nonfunctional spermatheca characteristic of parthenogenetic species that have no male.

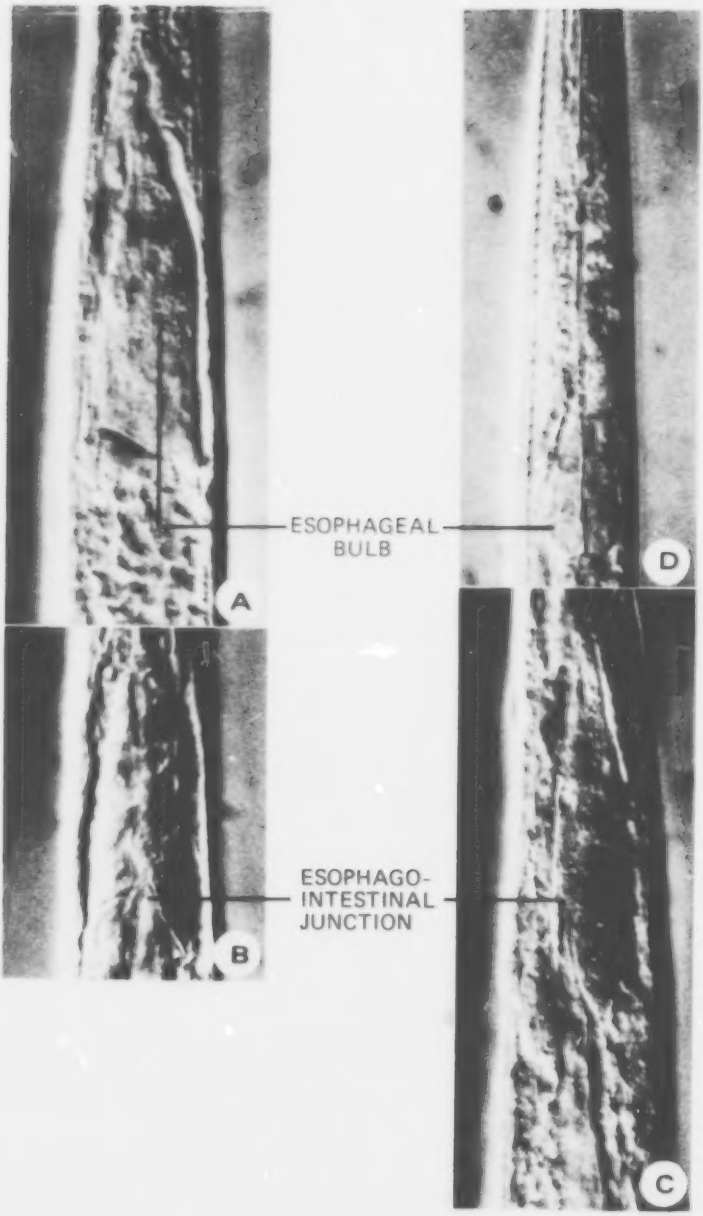


Fig. 39. *Ditylenchus destructor*. *A*, *B*, and *C*, Variation in form of the glandular esophageal bulb. In some species of genera, such as *Ditylenchus*, the esophageal bulb may overlap the intestine slightly, but never in long lobes. *D*, Typical form of the esophageal bulb in species of Tylenchidae.

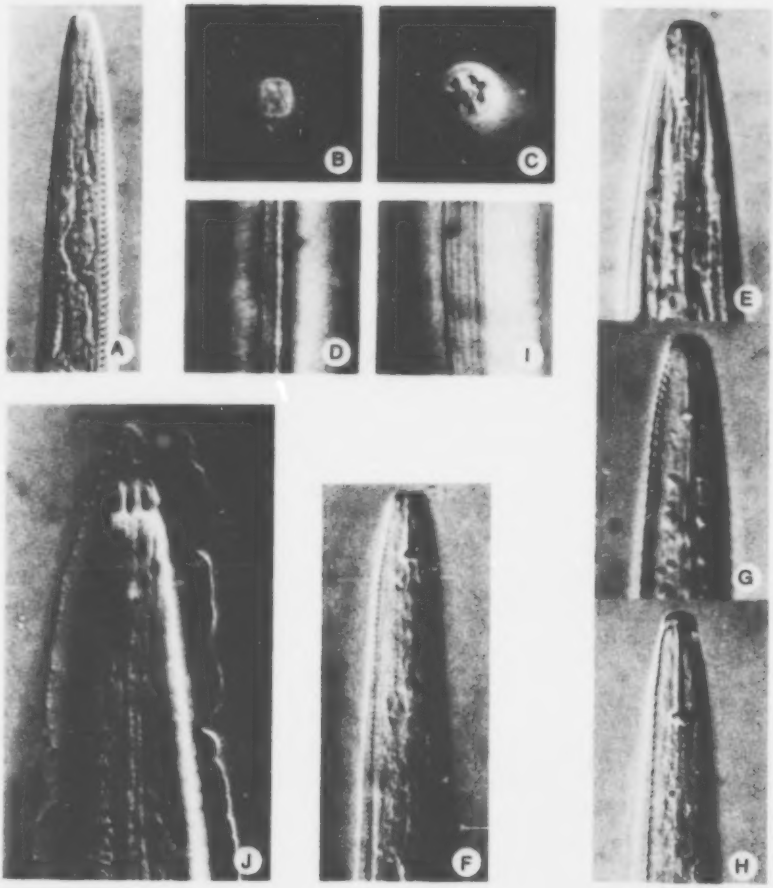


Fig. 40. *A*, Anterior end of an adult female of *Ottolenchus*. *B* and *C*, En face view of the heads of 2 females of *Ottolenchus* that are characterized by having 4 lips. *D*, Lateral field comprised of 2 incisures. *E* and *F*, Anterior ends of 2 species of *Tylenchus*. Note the regular size of the body annules. *G*, Anterior end of *Aglenchus* showing the characteristic coarse body annulation. *H*, Anterior end of *Cephalenchus*, which differs by having a head that is set off from the body by a constriction. Other species have heads that are continuous with the body, as shown in *A*, *E*, *F*, and *G*. *I*, Lateral field of *Cephalenchus* sp., which has 6 incisures. *J*, Anterior end of *Dactylotylenchus*. The unique head skeleton of species in this genus comprises finger-like projections and the cuticle adheres loosely to the head and body. The cuticle is not usually as separated as shown.

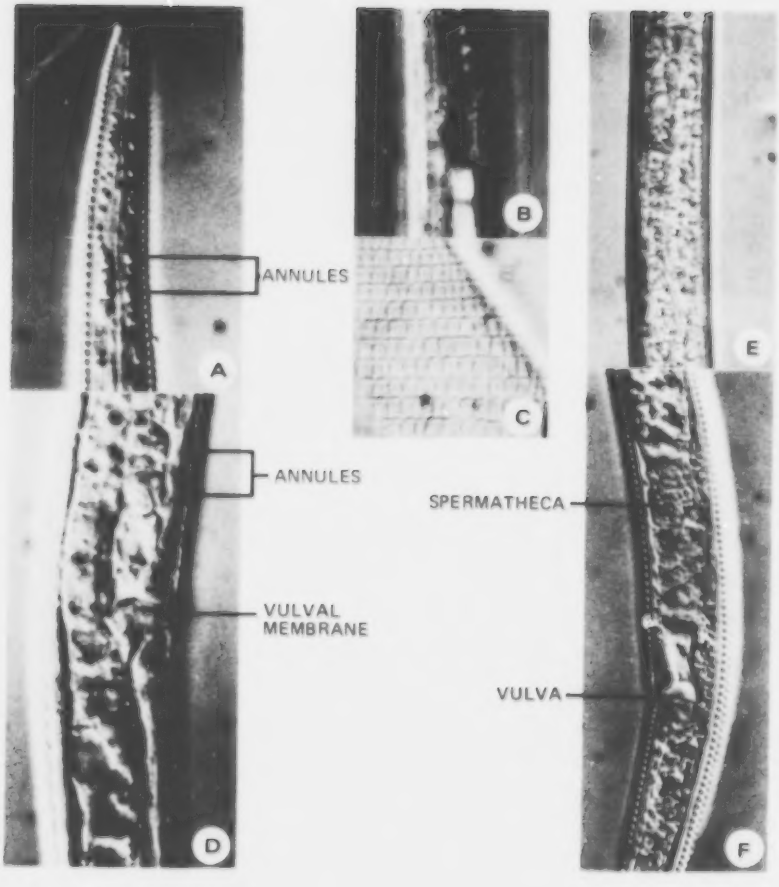


Fig. 41. *A*, Anterior end of *Aglenchus* illustrating the coarseness of annulation. *B*, In some species of *Aglenchus* common in Canada, the cuticle also has longitudinal striae (arrows) that divide the transverse striae into blocks, as shown in *C*. *D*, Lateral view of vagina of *Aglenchus* showing the characteristic lateral vulval membranes. *E* and *F*, Differences in annule widths in other species represented by *Tylenchus* (*E*) and *Ottolenchus* (*F*). Some species of *Tylenchus* (Fig. 15*B*) and *Ottolenchus* have rather coarse annules, but are distinct from *Aglenchus* by the absence of lateral vulval membranes, as in *F*.

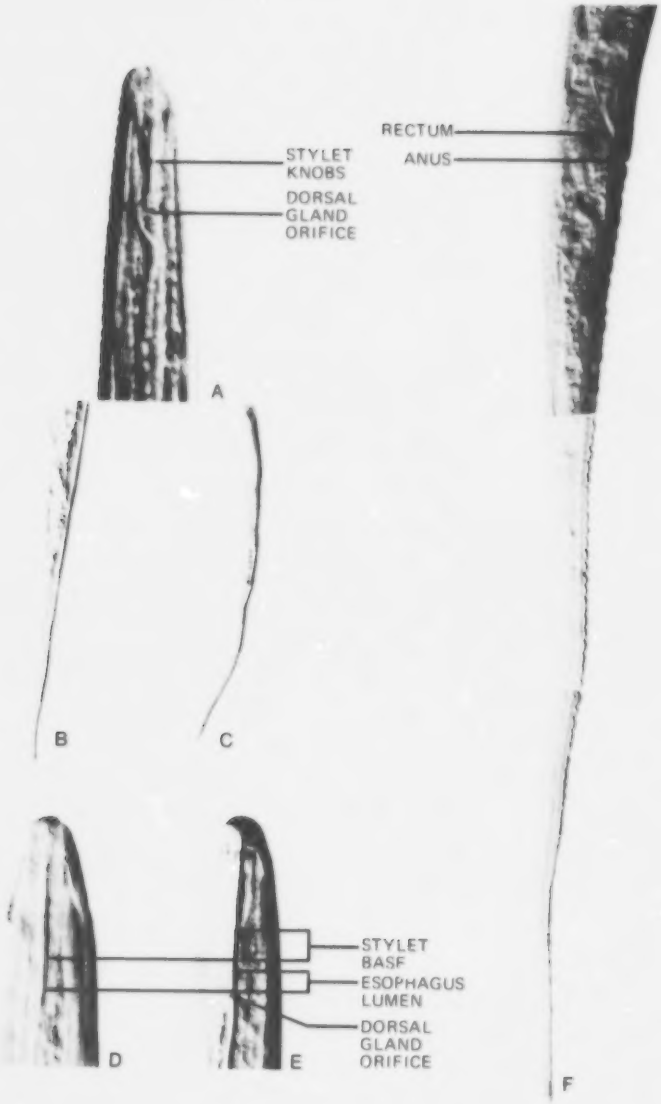


Fig. 42. *A*, Head of *Clavilenchus* sp. Species of this genus have a stylet with knobs, and the dorsal gland orifice is about 1 stylet length posterior to its base. *B*, Clavate tail terminus representative of species of *Clavilenchus*. *C*, Attenuated tail terminus typical of *Neopsilenchus* and some species of *Psilenchus*. *D* and *E*, Heads of *Psilenchus*. Note the posterior position of the dorsal gland orifice (*E*), which is usually close to the stylet base in most species of the Tylenchidae. *F*, Typical clavate tail of some species of *Psilenchus*, particularly *P. hilarulus*, a common terrestrial Canadian species.

Fig. 43. *Dolichodorus* sp. Adult, didelphic, amphidelphic female. Note the long, thin body characterizing species of this genus as compared to the average size of *Tylenchorhynchus* spp. (Fig. 45).

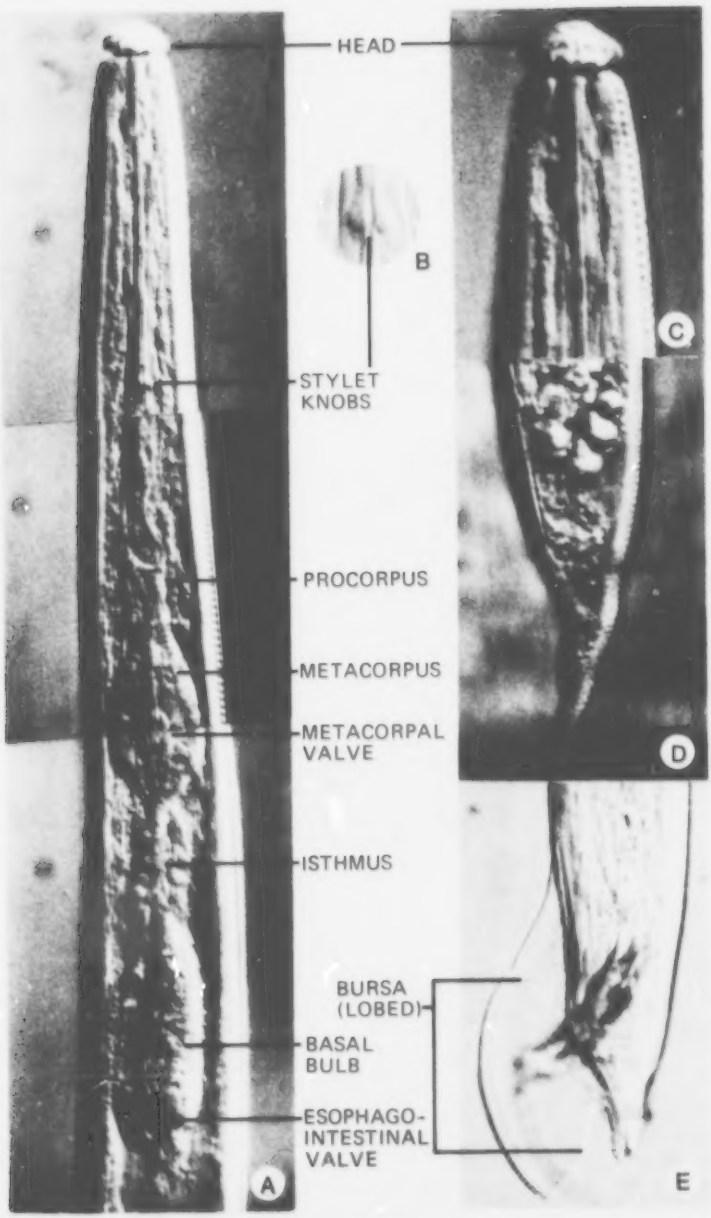


Fig. 44. *Dolichodorus* sp. *A*, Anterior end of female showing the structural features of the esophagus and stylet. *B*, Enlargement of stylet knobs, which slope posteriorly in this species. *C*, The head of this species, like all others of the genus, is prominently set off from the body by a deep constriction. *D*, Female tail. *E*, Male tail showing the diagnostic form of the lobed bursa.

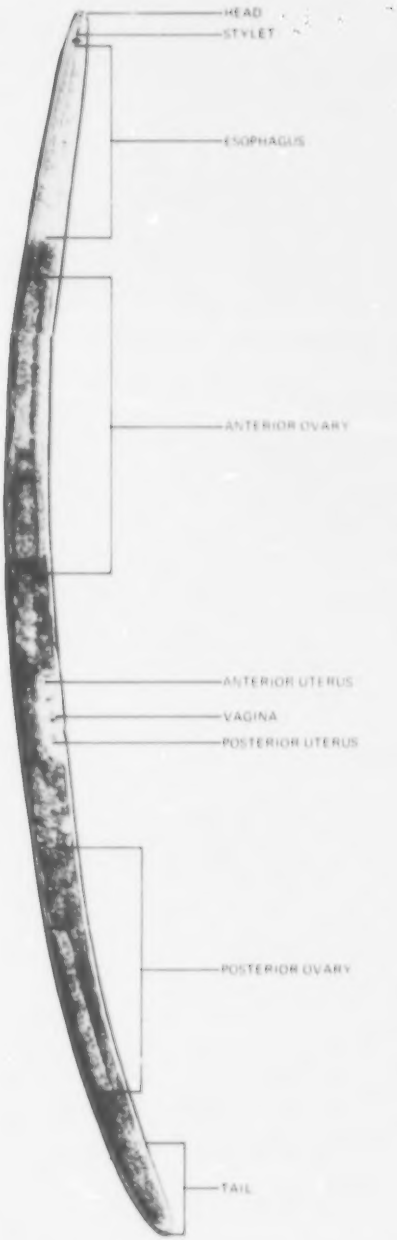


Fig. 45. *Tylenchorhynchus dubius*. Adult, didelphic, amphidelphic female illustrating the parts of the reproductive system. The size of this species (about 1 mm) is typical for members of the Tylenchorhynchidae.

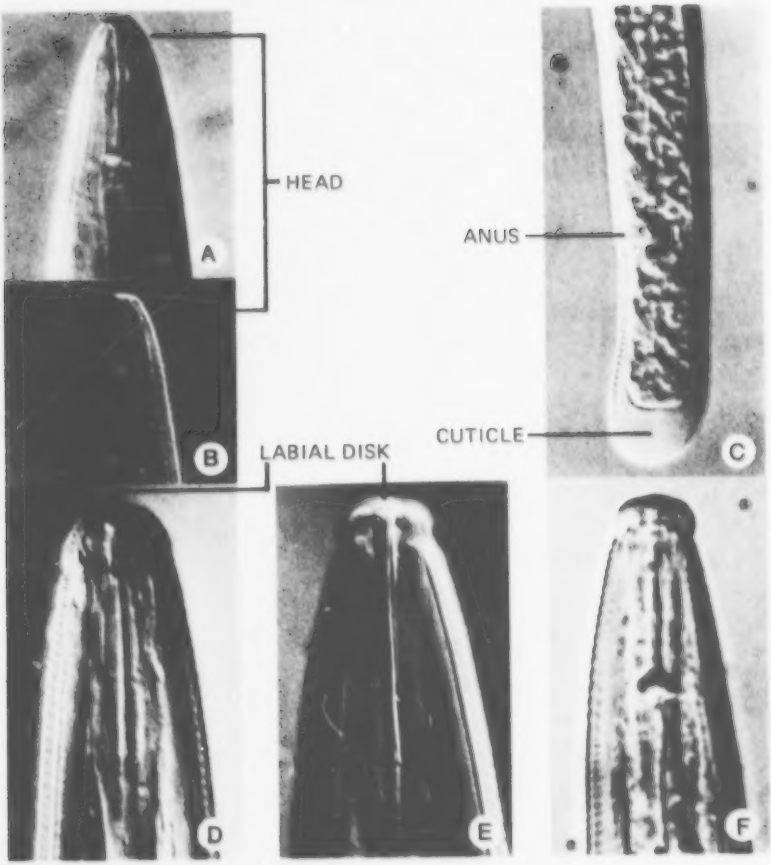


Fig. 46. *A* and *B*, Head ends of *Trophurus* sp. Although similar in body size and form to other Tylenchorhynchidae, the weakly developed head skeleton and stylet and the single, anterior ovary are atypical. *C*, Characteristic clavate tail of female of *Trophurus* sp. Note the unusually thickened cuticle at the tail terminus compared with those in Fig. 47*C*, *D*, *E*, and *F*. *D* and *E*, Head ends of 2 species of *Geocenamus* showing the prominent labial disk. *F*, A representative species of *Tylenchorhynchus* that does not have a labial disk.

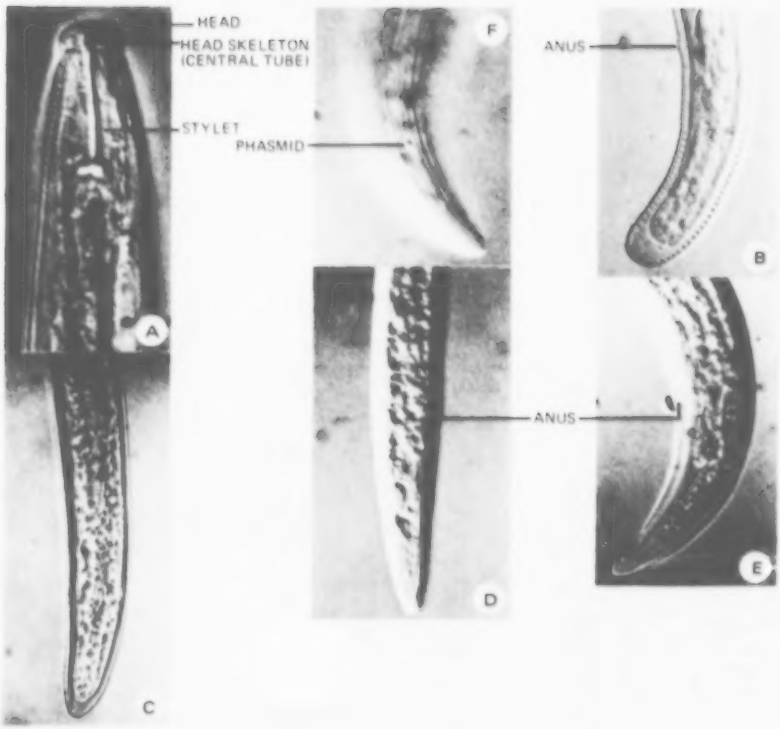


Fig. 47. *Tylenchorhynchus dubius*. *A*, Head and refractive parts of the head skeleton. *B*, *C*, *D*, and *E*, Range in tail shapes typical of species in the Tylenchorhynchidea, which includes cylindrical (*B*), subcylindrical (*C*, *D*), and conoid (*E*). *F*, Lateral field on tail showing a phasmid, which is located near the middle of the tail in these species. The length of the tail is often expressed as a ratio in relation to the anal body width. The tail is usually 2 to 3 times the anal body width in the Tylenchorhynchidae.

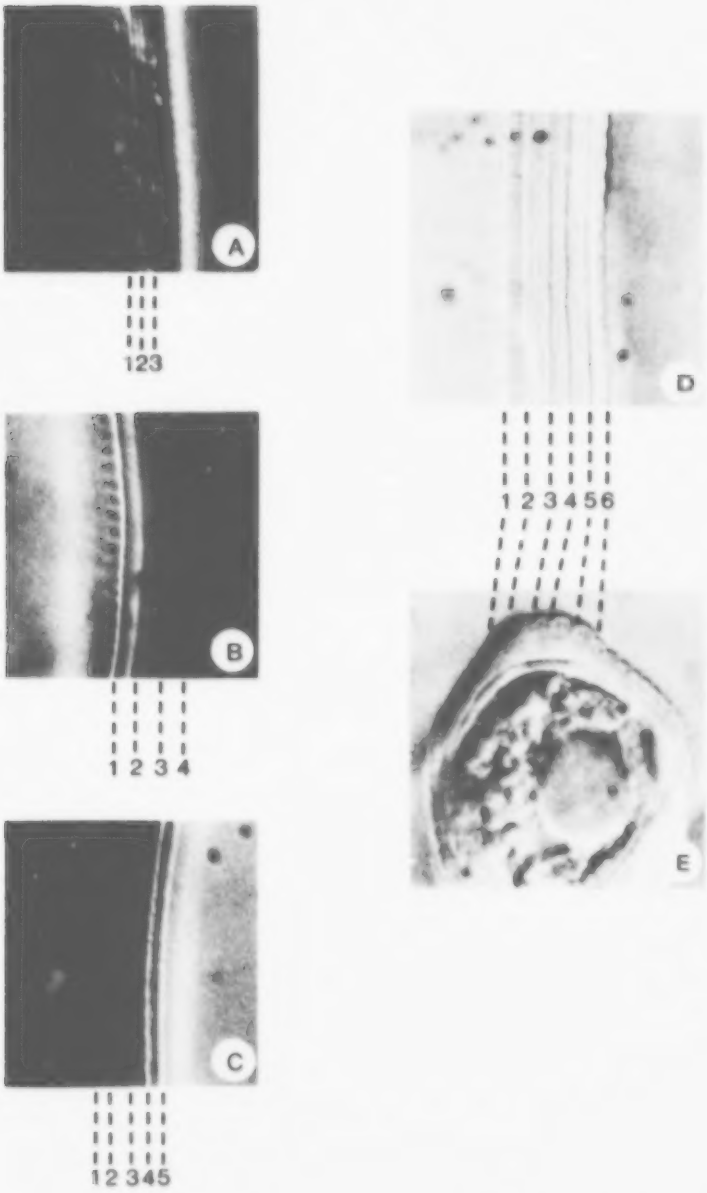


Fig. 48. Range in number of incisures in the lateral field of species in the Tylenchorhynchidae. *A* and *B*, *Tylenchorhynchus*. *C*, *Quinisulcius*. *D*, *Merlinius* and *Geocenamus*. *E*, Cross section near midbody showing the usual thickening of the cuticle at the lateral field and number of incisures. In some species of nematodes the incisures are obscure and cross sections are required to determine the number.

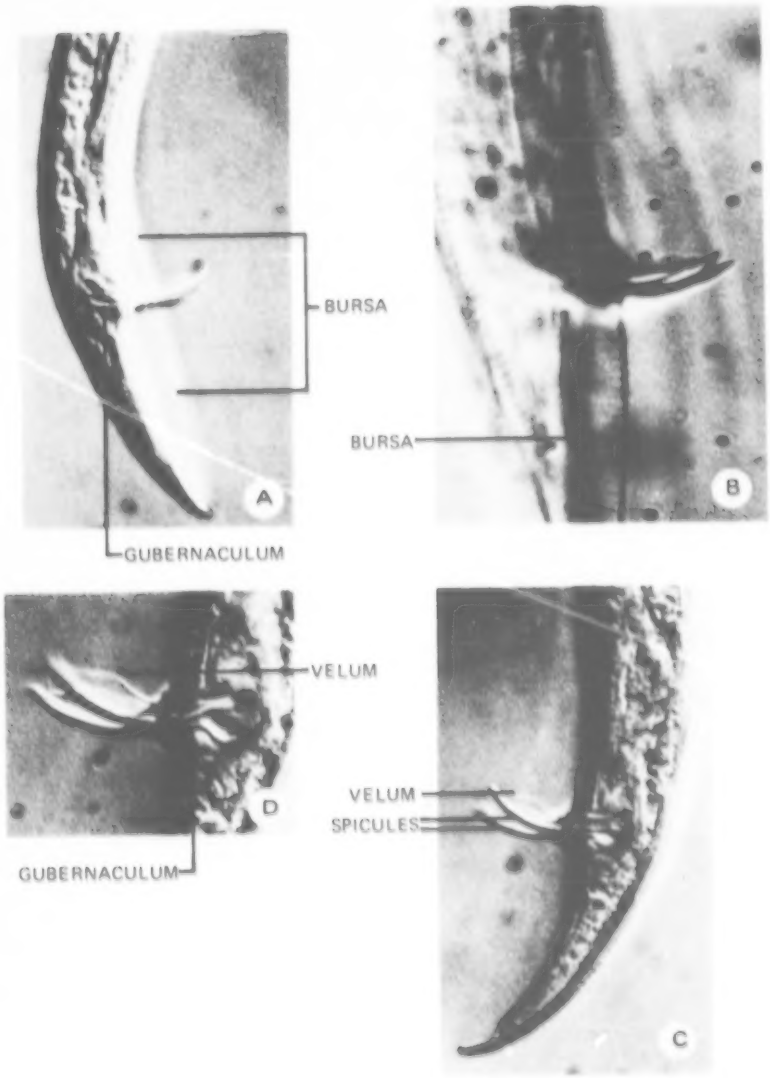


Fig. 49. *A* and *B*, Male tails characterizing the genus *Tylenchorhynchus*. *C* and *D*, Lateral view of the paired spicules, which are extended as they are during copulation. Note the structure of the spicules, particularly the thin membranous velum along the ventral surfaces. The long gubernaculum is typically linear (*A*) but may occasionally be bent (*D*) when the spicules are extended.

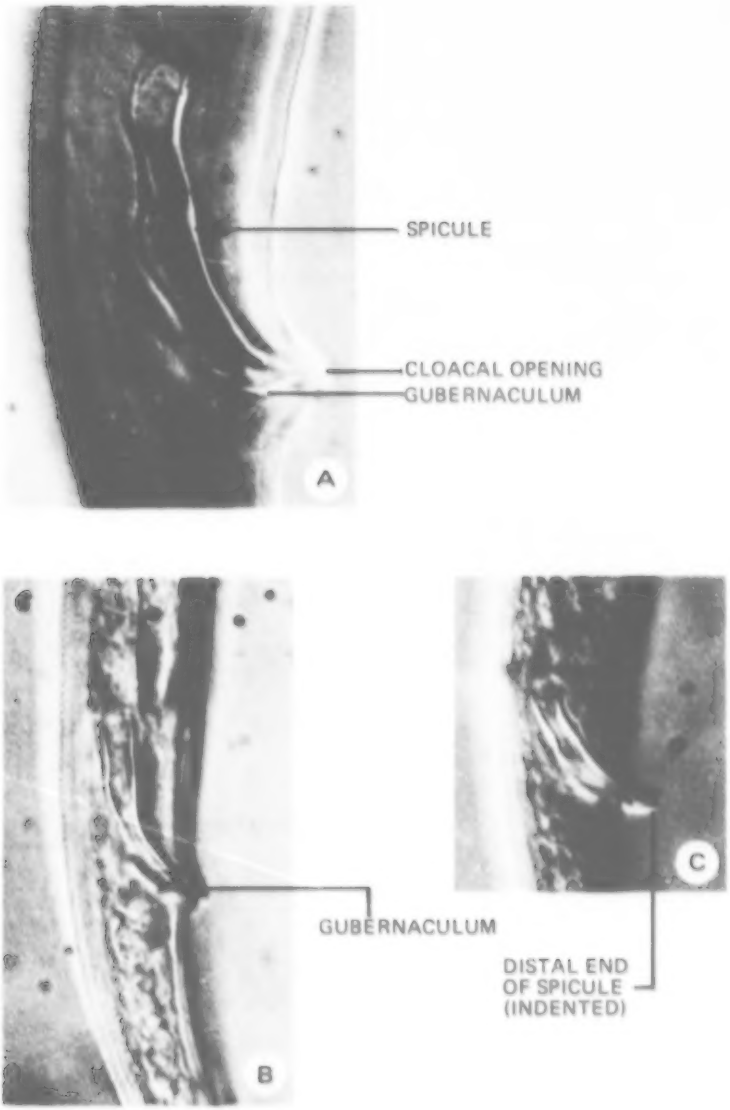


Fig. 50. Male tails characterizing the genus *Merlinius*. Note the diagnostically heavy sclerotization along the ventral surface of one of the paired spicules, the absence of a velum, and the indentation of the distal end (*C*). The gubernaculum in these species is short and arcuate when contrasted with the gubernaculum in *Tylenchorhynchus* (*see* Fig. 49*D*).

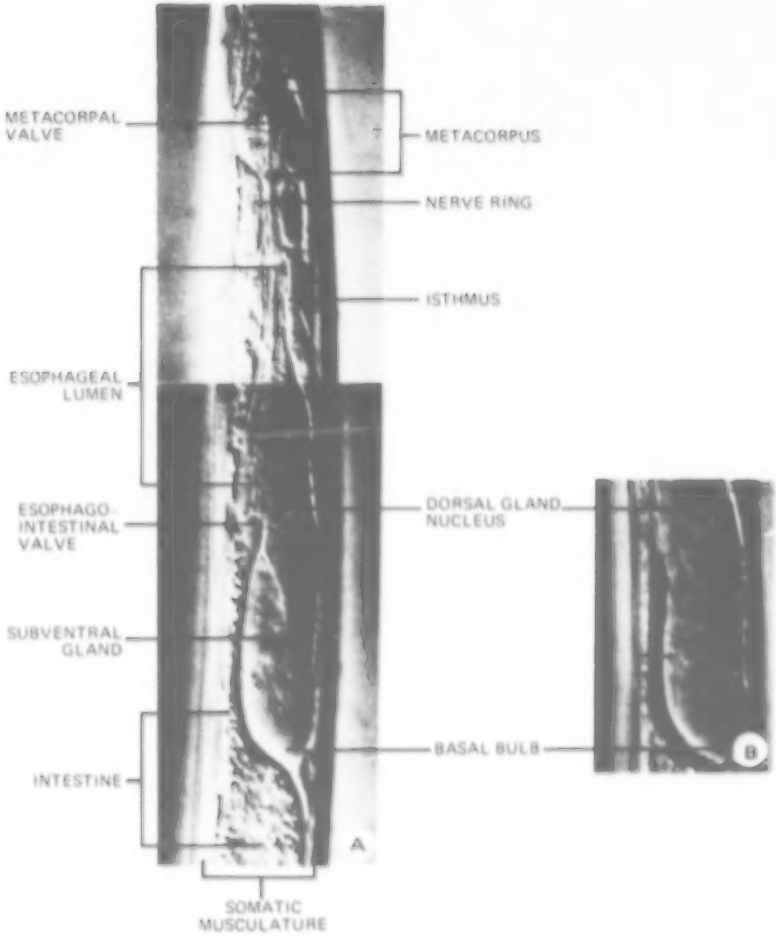


Fig. 51. *A*, Example of an esophagus of the Pratylenchidae having the glands extending over the intestine in long lobes. *B*, Enlargement of the glands showing the dorsal and one of the two subventral gland nuclei (arrow). Note the coarse, granular contents of the intestine and homogeneous, transparent texture of the esophageal glands. This contrast in refractiveness is conspicuous at the lower magnifications of the dissecting microscope, facilitating separation of plant-parasitic species with overlapping glands from those with apposing glands (*see* Fig. 15) in mixed populations.

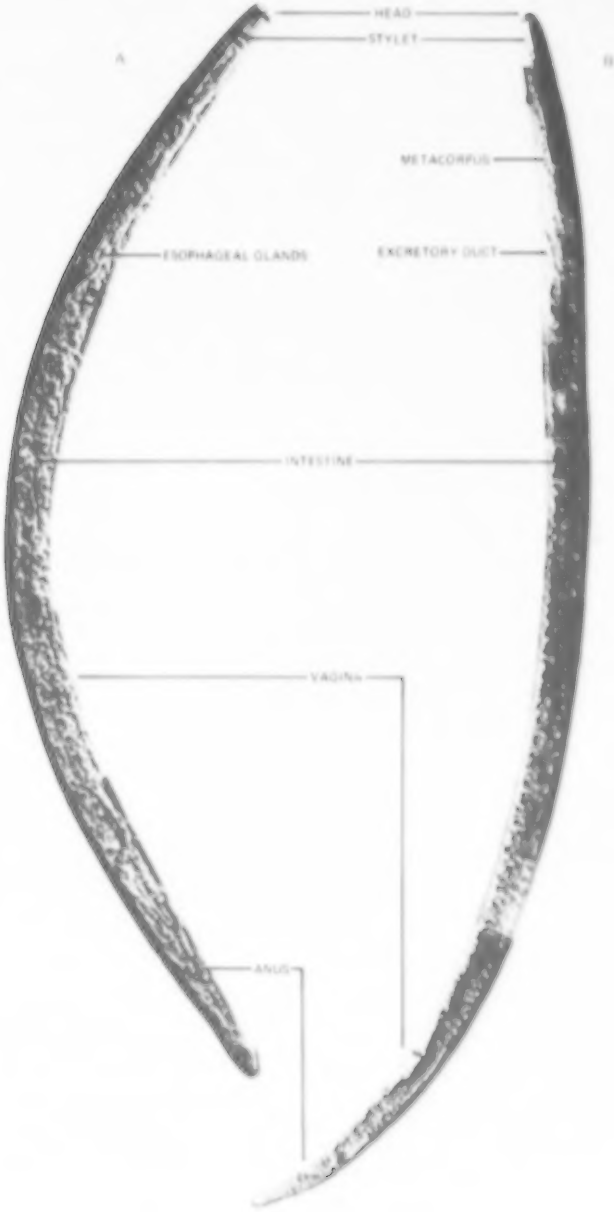


Fig. 52. *A*, A didelphic, amphidelphic female of *Pratylenchoides*. *B*, A monodelphic, prodelphic female of *Pratylenchus*. Being similar in body proportions and morphology, the position of the vagina and the presence of 1 (*B*) or 2 (*A*) ovaries are important characteristics for separating the species of these genera.

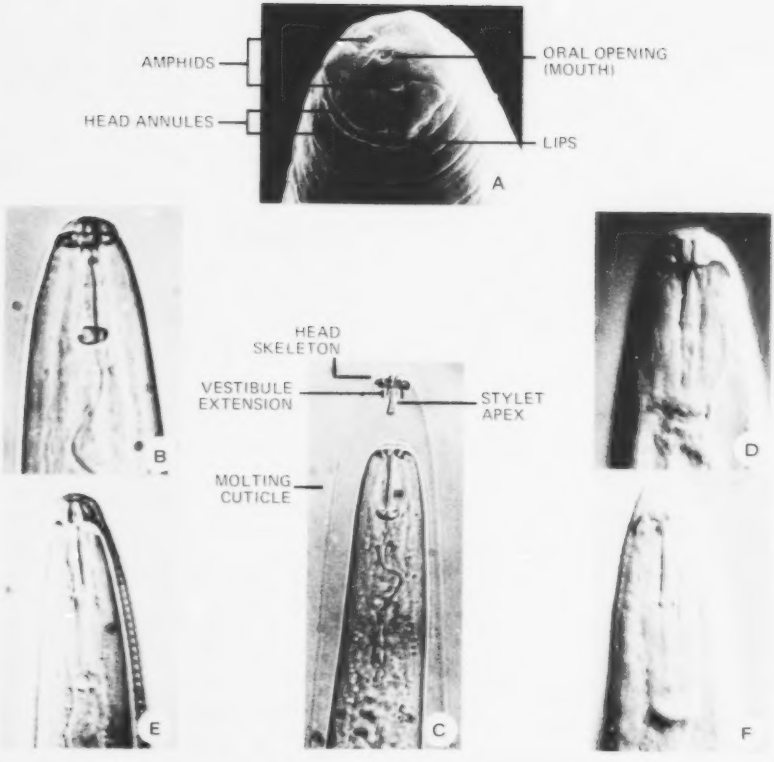


Fig. 53. *A*, Scanning micrograph of the head of *Pratylenchus* sp. showing the typical form of the lips for some, but not all, of the root-lesion nematodes. Also shown are the amphid apertures and oral opening through which the stylet projects during feeding. Note that the small lateral lips are separate, whereas the usual pair of subdorsal and subventral lips are fused as in Fig. 35*A*. *B*, Lateral view of the head of *Pratylenchus* sp. illustrating the low, flattened profile characteristic of the Pratylenchidae. *C*, Molting of a species of *Pratylenchus*. In nematodes, the head skeleton, stylet apex, and vestibule extension (*see also* Fig. 80*C*) are shed with the cuticle. *D*, The head of *Hirschmanniella* spp. is very broad and low, but not as flattened as in *Pratylenchus* spp. *E* and *F*, Head shapes of species representative of the Hoplolaimidae for comparison. Most species in other families have a high rounded (*E*) or truncated (*F*) head that equals or exceeds its width.

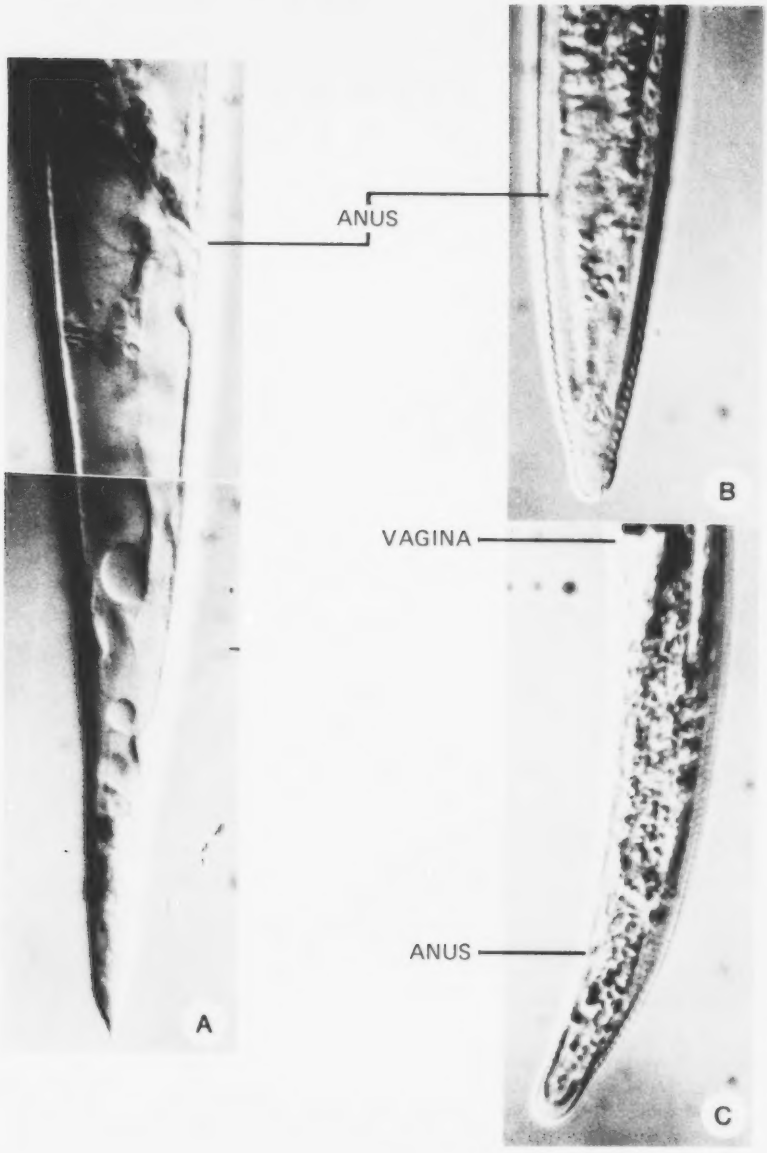


Fig. 54. Adult female tail of *Hirschmanniella* (*A*), *Pratylenchoides* (*B*), and *Pratylenchus* (*C*). The long tail with a sharply attenuated terminus (mucronate) of *Hirschmaniella* immediately separates these species from those of the other genera in Pratylenchidae.

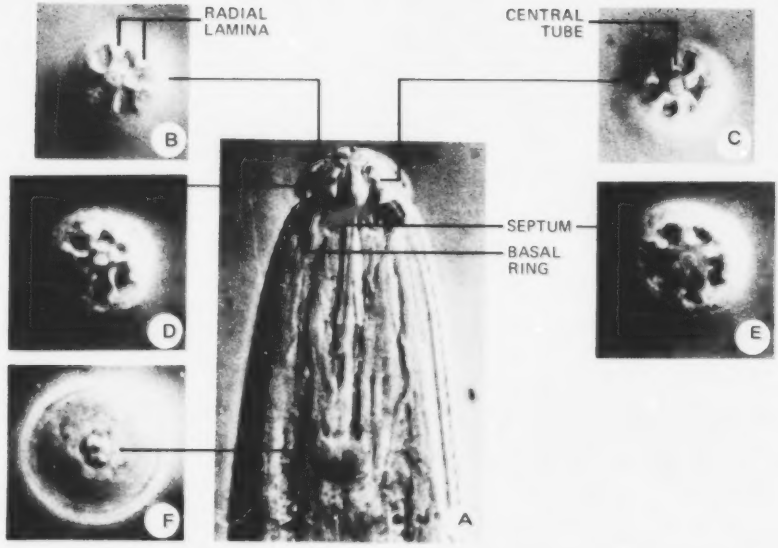


Fig. 55. Structure of the head skeleton of a plant-parasitic nematode as represented by one of the lance nematodes, *Hoplolaimus galeatus*. *A*, Side view of head showing the "massive" structure of the radial lamina and basal ring. *B*, *C*, *D*, and *E*, Progressive series of cross sections to the basal ring showing the continuity of the central tube and the 6 radial lamina. The lamina gradually thicken posteriorly, joining the basal ring to form a plate or septum (*E*). The basal ring extends into the body and serves as an attachment point for the stylet and somatic musculature. *F*, Cross section through the stylet knobs, typically 3, to which the protractor muscles are attached.

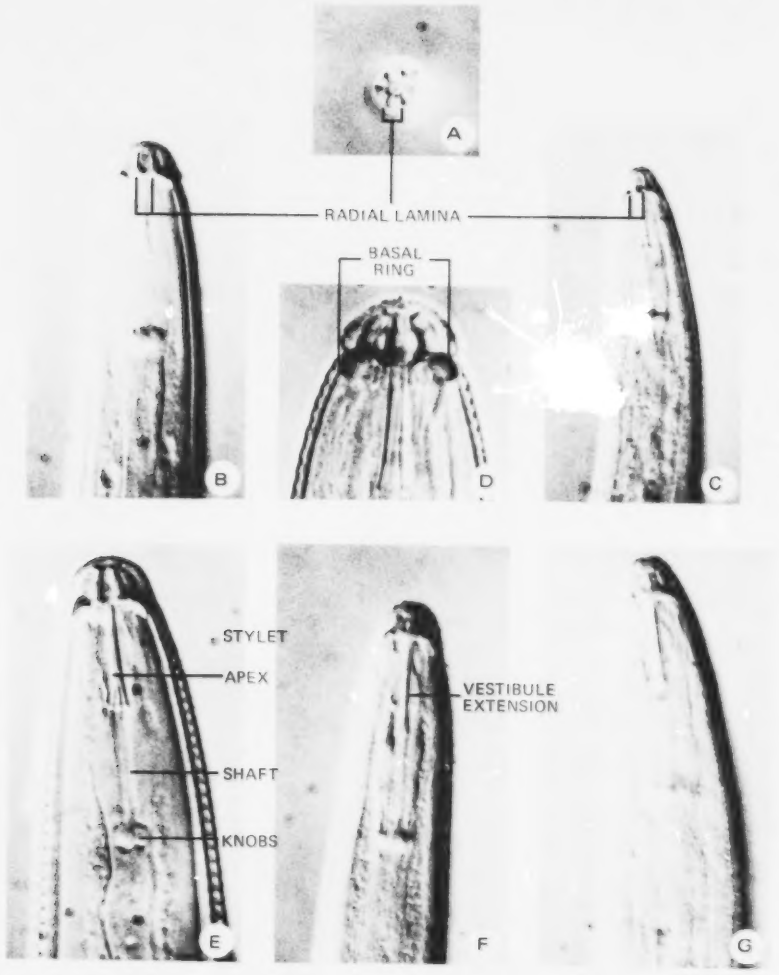


Fig. 56. Examples of the diagnostic head shapes and skeletal development in species of the Hoplolaimidae (*compare with* Figs. 14*A*, *C*; 34*B*, *C*, *D*, *E*; 40*E*, *F*, *G*, *H*; 41*A*). *A*, *Scutellonema brachyurum*. *C* and *G*, *Helicotylenchus canadensis*. *D*, *Hoplolaimus glaeatus*. *E*, *Rotylenchus fallorobustus*. *F*, *Helicotylenchus platyurus*. *B*, En face view (*B*) and side views (*A*, *C*) of head skeleton showing the radial lamina. The heads of most species are continuous with the body, but may be set off by a constriction (*D*). Arbitrary terms are often used to characterize the skeleton, such as weak, moderate, strong, and massive. These terms reflect differences in thickness of the lamina and basal ring.

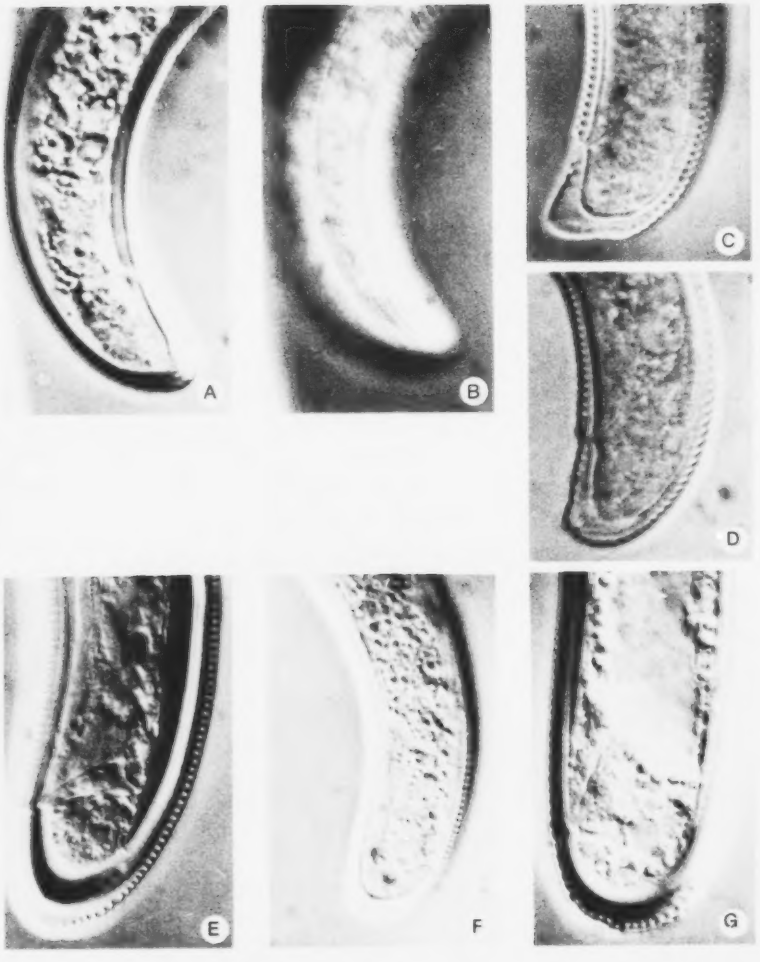


Fig. 57. Sizes and shapes of female tails of the species in the Hoplolaimidae. The short tail, characteristic of the family, is about equal to or less than the anal body width. *A*, *C*, and *D*, *Helicotylenchus* spp. having convex-conoid tails. *B*, Lateral field on tail of *H. platyurus* (*A*) showing a phasmid (arrow) slightly anterior to the anus. *E*, *Rotylenchus*. *F*, *Scutellonema*. *G*, *Hoplolaimus*. Species having broadly rounded (*E*, *F*) and hemispherical (*G*) tails are particularly common in *Rotylenchus*, *Scutellonema*, and *Hoplolaimus*.

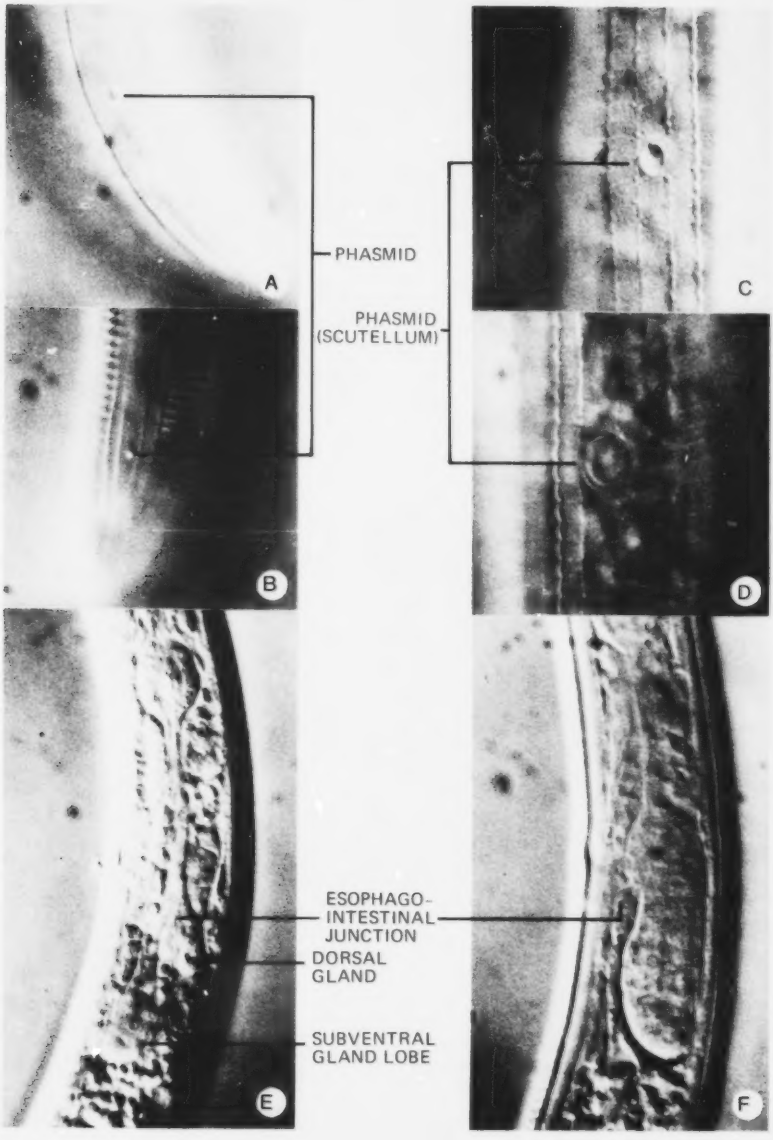


Fig. 58. *A* and *B*, Typical small phasmids of *Rotylenchus* and *Helicotylenchus*. *C* and *D*, Large phasmids or scutella characteristic of *Hoplolaimus* and *Scutellonema*. *E*, Form of the overlapping glands of *Helicotylenchus*. Note that the esophagointestinal valve is axial and that the subventral glands extend ventrally over the intestine. *F*, Form of the overlapping glands in *Rotylenchus*, *Hoplolaimus*, and *Scutellonema*. In these genera, the esophagointestinal valve is set off ventrally and the glands overlap the intestine dorsally.

Fig. 59. Adult female of *Scutellonema* showing the characteristic body shape of the genus when relaxed.

Fig. 60. Adult female *Helicotylenchus platyurus*. The spiral form of the relaxed female is a characteristic of the genus and also of several species of *Rotylenchus*.

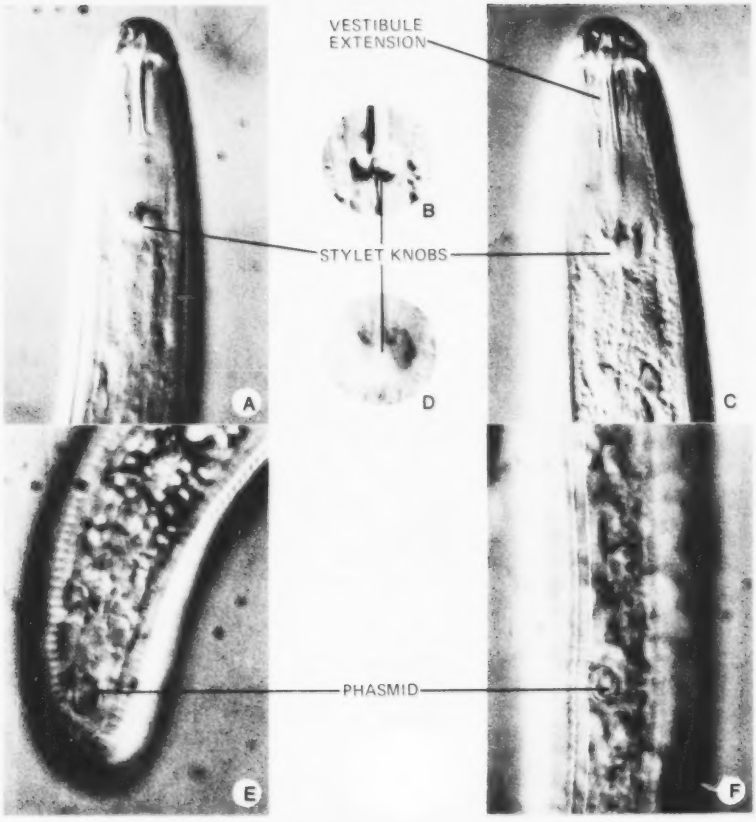


Fig. 61. *A*, Head of *Scutellonema*. *B*, Rounded stylet knobs. *C*, Head of *Hoplolaimus*. *D*, Stylet knobs with anterior projections. Note the diagnostic differences in the shape of the stylet knobs characteristic of these genera. *E*, Phasmid or scutellum located on the tail of *Scutellonema*. *F*, Phasmid or scutellum in the lateral field on body of *Hoplolaimus* anterior to the vulva. The phasmid on the opposite lateral side is always located posterior to the vulva at some distance from the tail in the lance nematodes.

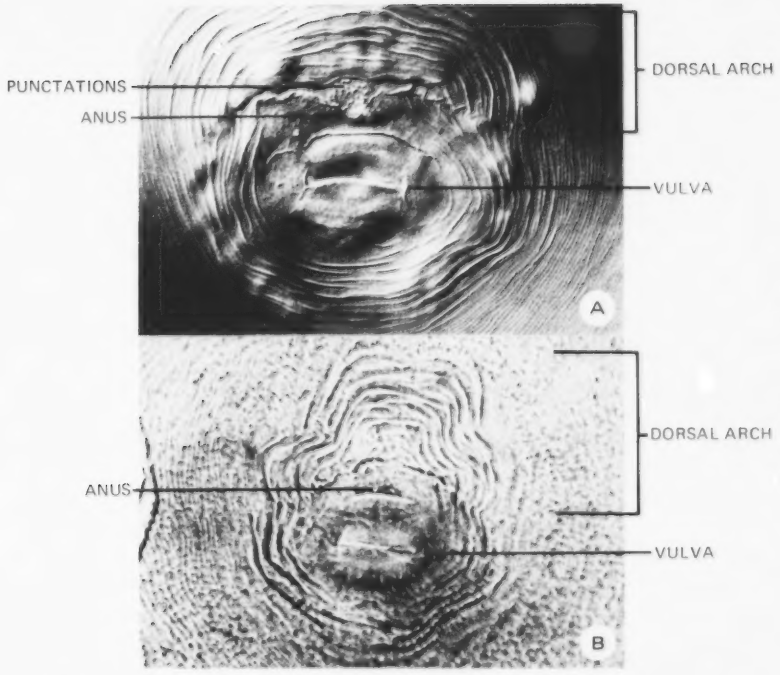


Fig. 62. Perineal patterns of 2 root-knot species, *Meloidogyne hapla* (*A*) and *M. microtyla* (*B*). Note the absence of punctations in *M. microtyla* and the low dorsal arch characteristic of *M. hapla* as compared with the high dorsal arch in *M. microtyla*.

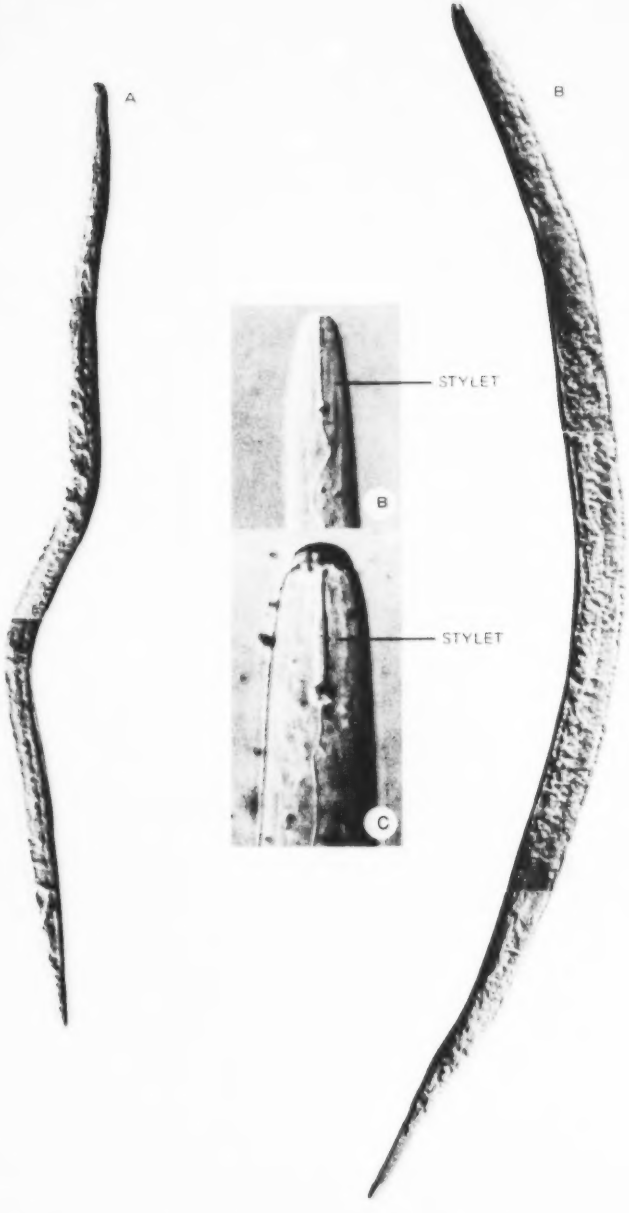


Fig. 63. Second stage infective larvae or juveniles of *Meloidogyne* (*A*, *B*) and *Heterodera* (*C*, *D*). Note the marked differences in size and development of the heads and stylets and in body size. Mixed populations of the infective larvae of these 2 genera can be readily distinguished by these larval characteristics.

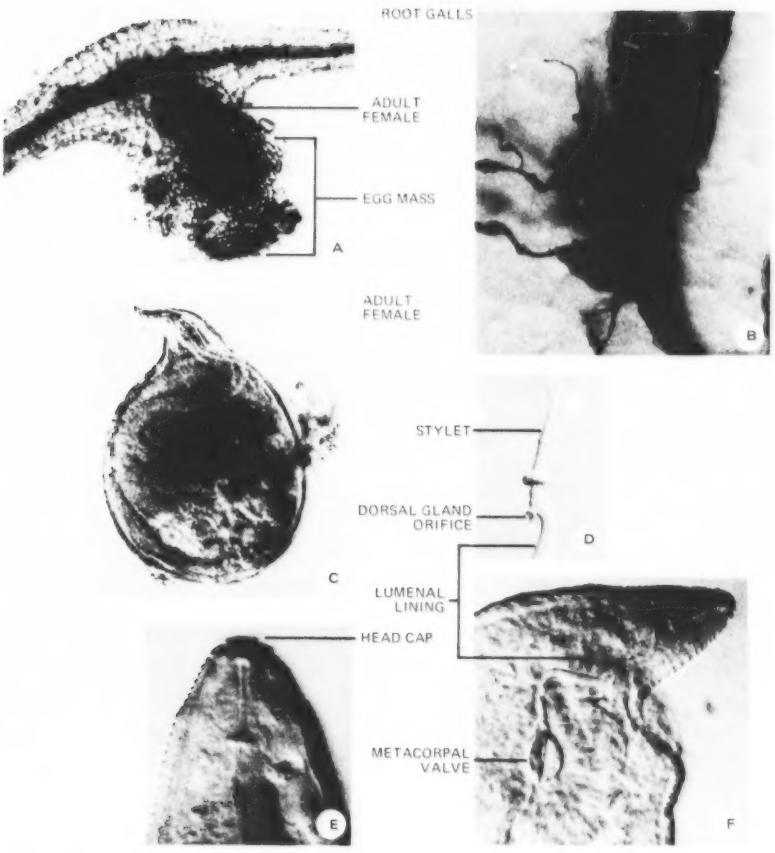


Fig. 64. Adult sedentary female (endoparasite) of *Meloidogyne*. *A*, Adult female embedded in a root gall showing a large egg mass contained in a gelatinous matrix external to the root. *B*, Large, compounded root galls produced by numerous females within the root. *C*, Adult female illustrating the thin, soft body cuticle. *D*, Excised stylet showing continuity with the cylindrical lumenal lining of the esophagus and the dorsal gland orifice through which the salivary secretions are emitted. *E*, Head of swollen female showing the diagnostic head cap. *F*, Anterior end of swollen female. Note the massive metacorpal valve that functions as a pump during feeding.

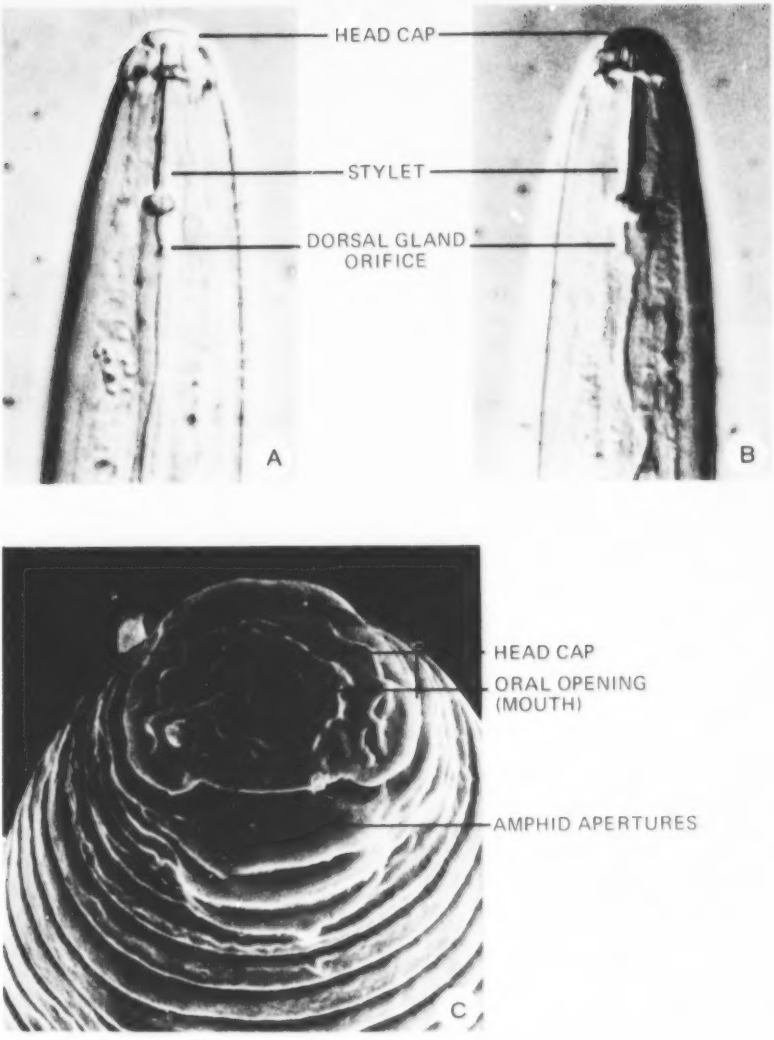


Fig. 65. Adult male of *Meloidogyne*, the root-knot nematode. Anterior end showing the head cap and stylet from a dorsoventral view (*A*) and a lateral view (*B*). Scanning micrograph (*C*) of the head. Note the large elongated amphid apertures along the lateral sides of the head cap, which are a conspicuous feature at lower magnifications (*A*). The presence of a head cap and the large, elongate amphid apertures readily separate the males of *Meloidogyne* from those of *Heterodera*, *Punctodera*, and *Globodera*, which lack a head cap and have small, oval amphid apertures (*see* Fig. 67*A*, *B*).

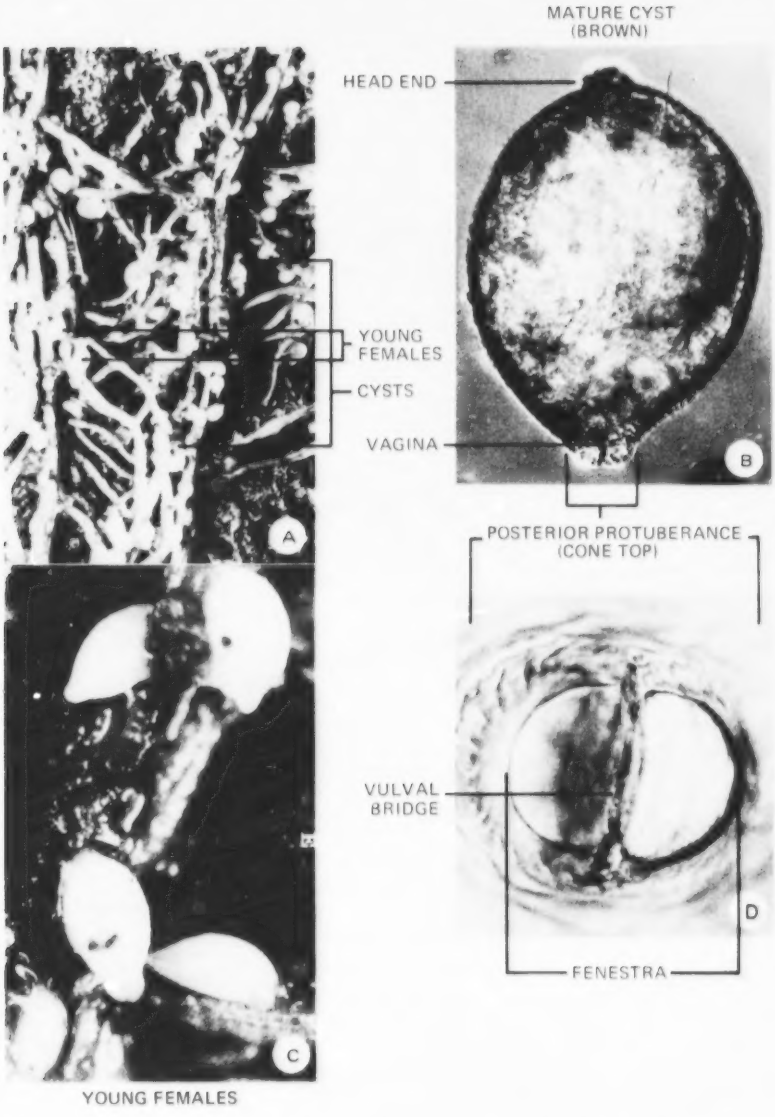


Fig. 66. White (living) females and cysts of *Heterodera*. *A* and *C*, Females and cysts on plant roots with the neck typically embedded within the root tissue. *B*, A mature cyst, which is generally lemon-shaped and has a hard outer covering. *D*, Cone top of cyst showing the diagnostic structure of the fenestra. *Meloidogyne* females never form a cyst and remain mostly embedded in the root tissue. *Heterodera*, *Punctodera*, and *Globodera* females transform into a cyst and only the head end remains embedded in the root tissue.

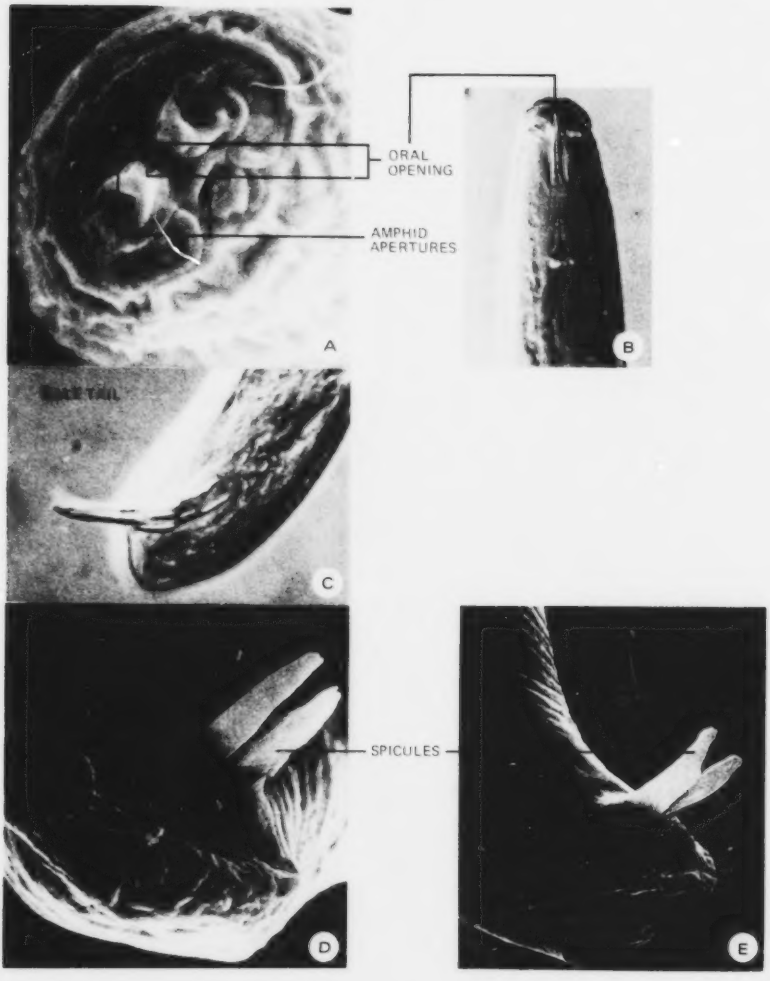


Fig. 67. *A*, *B*, and *C*, Cyst nematodes. Scanning micrograph of the head (*A*). Note the small amphid apertures characterizing the male cyst nematodes as contrasted with the root-knot species (*see* Fig. 65*C*). Lateral view of male head (*B*), which does not have a head cap like the root-knot species (*see* Fig. 65*A*, *B*). Lateral view of the male tail (*C*) with spicules extended. *D* and *E*, Root-knot nematodes. Scanning micrographs of a lateral view (*D*) of the male tail and of the extended spicules (*E*). As in the cyst nematodes, the males lack a bursa and the cloacal opening is near the tail terminus.

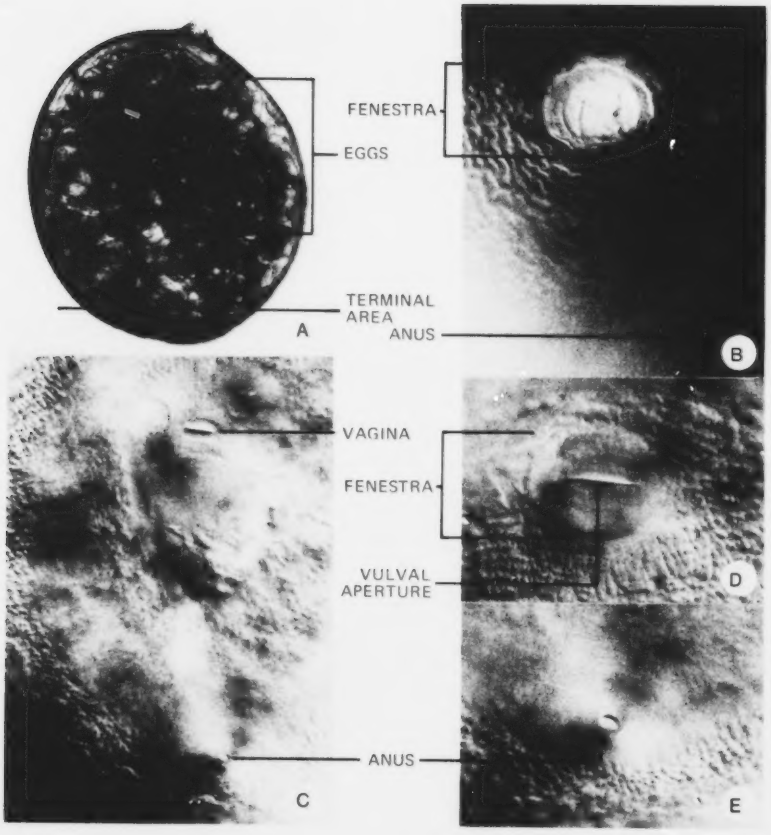


Fig. 68. *Globodera*. *A*, Mature cyst, typically round, showing the characteristic hard outer covering, which is usually light to dark brown, and the long neck. The eggs are retained within the cyst and may remain viable for several years in the soil in the absence of host plants. Hatching and penetration of the infective, 2nd stage larvae are promoted by exudates from the roots of host plants. *B*, Terminal area of a mature cyst. In the mature cyst the thin, fenestral area disintegrates to form a hole that allows the hatching larvae to escape. *C*, *D*, and *E*, Terminal area of white female showing the spatial relationship between the vulva and anus (*C*) and the diagnostic features of the vulva (*D*) and anus (*E*). Note that the anus lacks a fenestra.

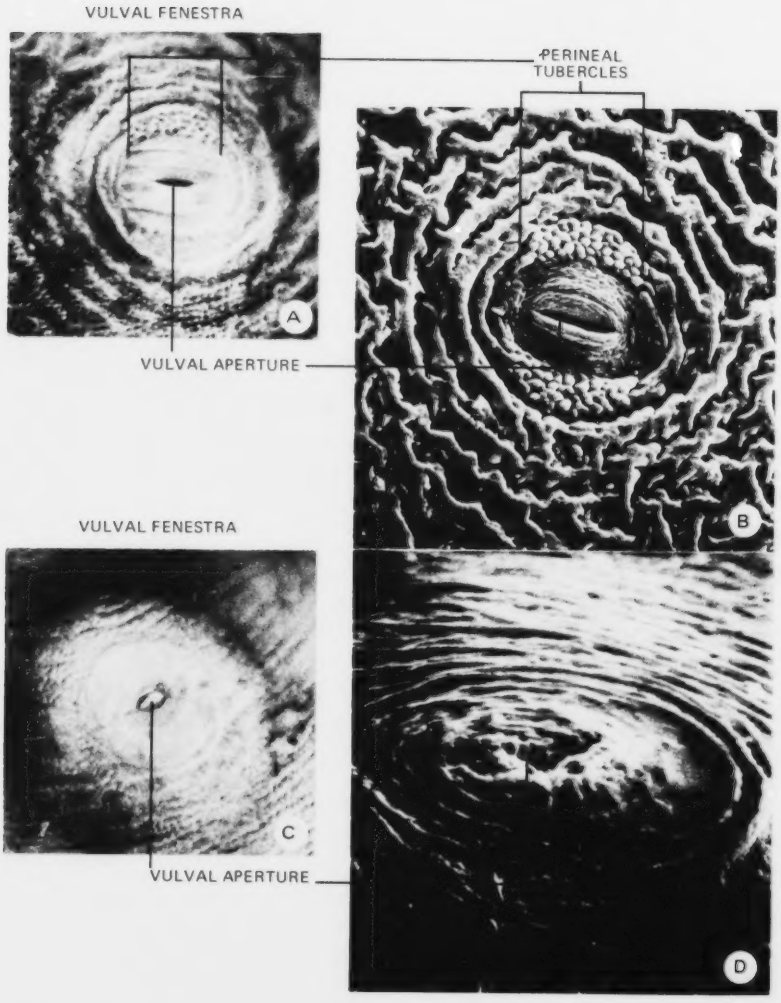


Fig. 69. *A* and *B*, *Globodera* female. Terminal area (*A*) showing surface and subsurface features of a white female. Scanning micrograph (*B*) of the terminal area resolving details of the perineal tubercles. *C* and *D*, *Punctodera* female. Terminal area (*C*) of a white female showing surface and subsurface features. Scanning micrograph (*D*) showing the uniformity in structure of the terminal area. Females of *Globodera* and *Punctodera* are readily identified by the presence or absence of perineal tubercles, which are most pronounced in the white female.

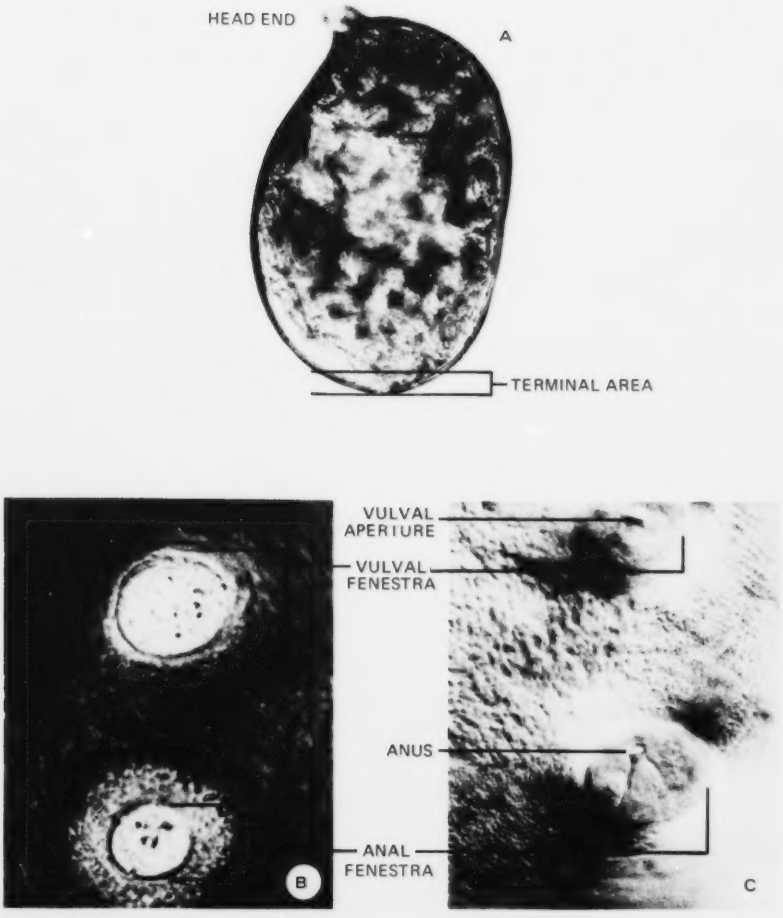


Fig. 70. *Punctodera*. *A*, Mature, pear-shaped cyst having a characteristically short neck. *B*, Terminal area of mature cyst showing the vulval and anal fenestra. *C*, Terminal area of young white female. Note that the vulval and anal fenestra are about equal in size. Species of *Punctodera* are easily distinguished from those of *Globodera* (*see* Fig. 68*C*), which lack an anal fenestra.

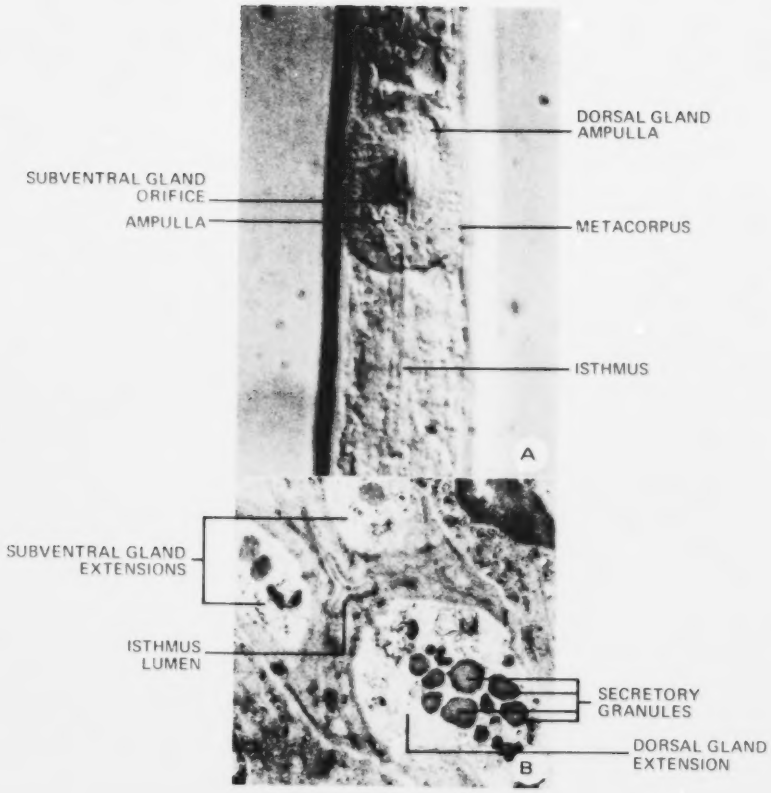


Fig. 71. *A*, Representative metacorpus of the aphelenchid parasites (suborder Aphelenchina) showing the dorsal and 1 of the 2 subventral glands ending in the metacorpus (*see* Key no. 1). In the tylenchid parasites (suborder Tylenchina), the dorsal gland exits into the esophageal lumen through a conspicuous, peg-like duct near the base of the stylet (*see* Figs. 2, 4*A*, 64*D*, 67*B*). *B*, Electron micrograph of a cross section of the isthmus showing the dorsal and 2 subventral gland extensions. Proteinaceous secretion granules produced in the glands are transported anteriorly to the terminal ducts, as seen in a subventral gland ampulla in *A*, where they breakdown and release digestive enzymes.

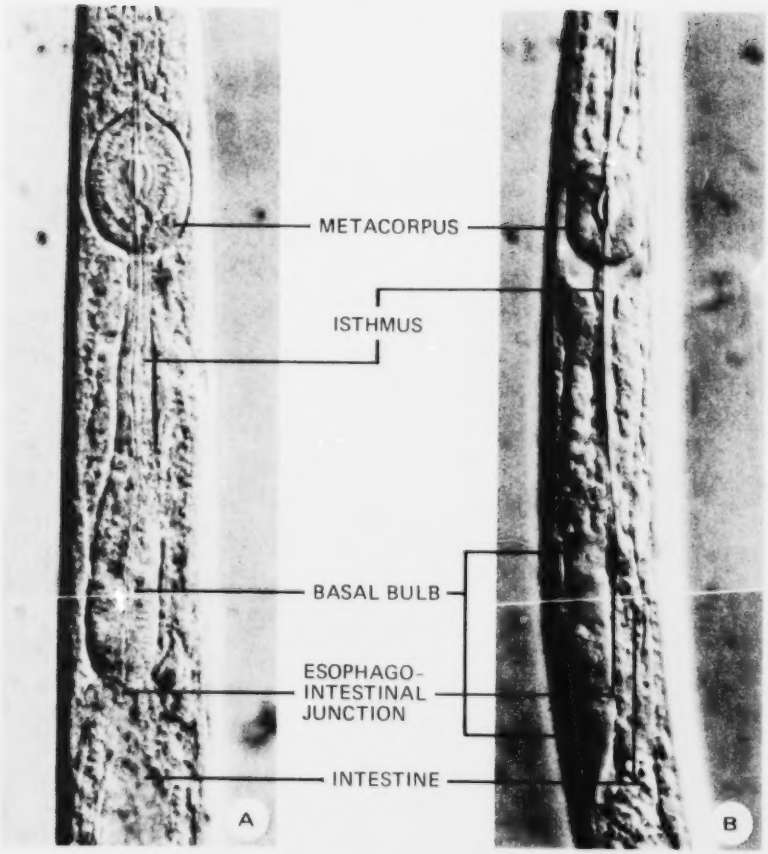


Fig. 72. *A*, *Paraphelenchus*. The esophageal glands are contained in a basal bulb that does not overlap the intestine. *B*, *Aphelenchus*. The esophageal glands in this and other genera of aphelenchids overlap the intestine in long lobes. Note the typically massive size of the metacorpus, which occupies the entire width of the body cavity, in contrast to most of the tylenchids (*see* Figs. 2; 15*A*, *B*; 40*A*; 58*E*).

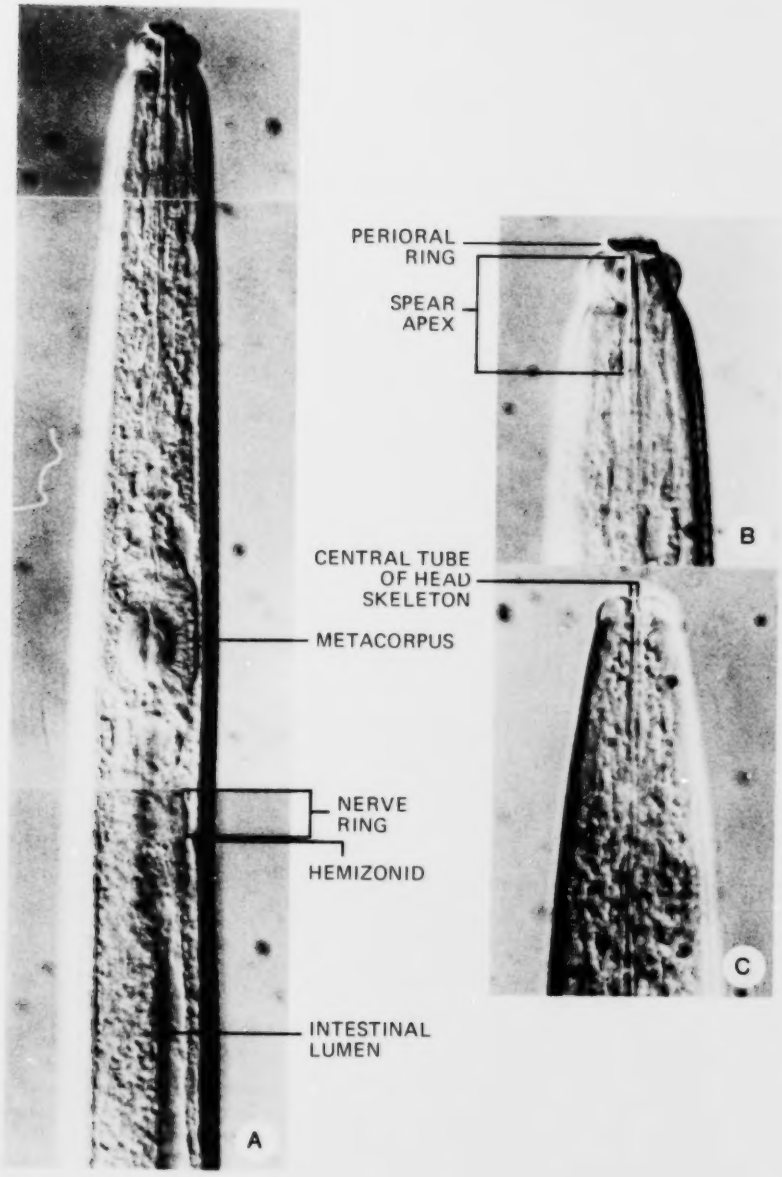


Fig. 73. *A*, Anterior body of *Anomyctus*. *B*, Head of *Anomyctus*. Note the bulbous, set-off head and the diagnostic perioral ring. *C*, By contrast, the heads of many aphelenchids are continuous with the body and are smoothly rounded. Note the prominence of the head skeleton central tube, which is a diagnostic feature of some genera.

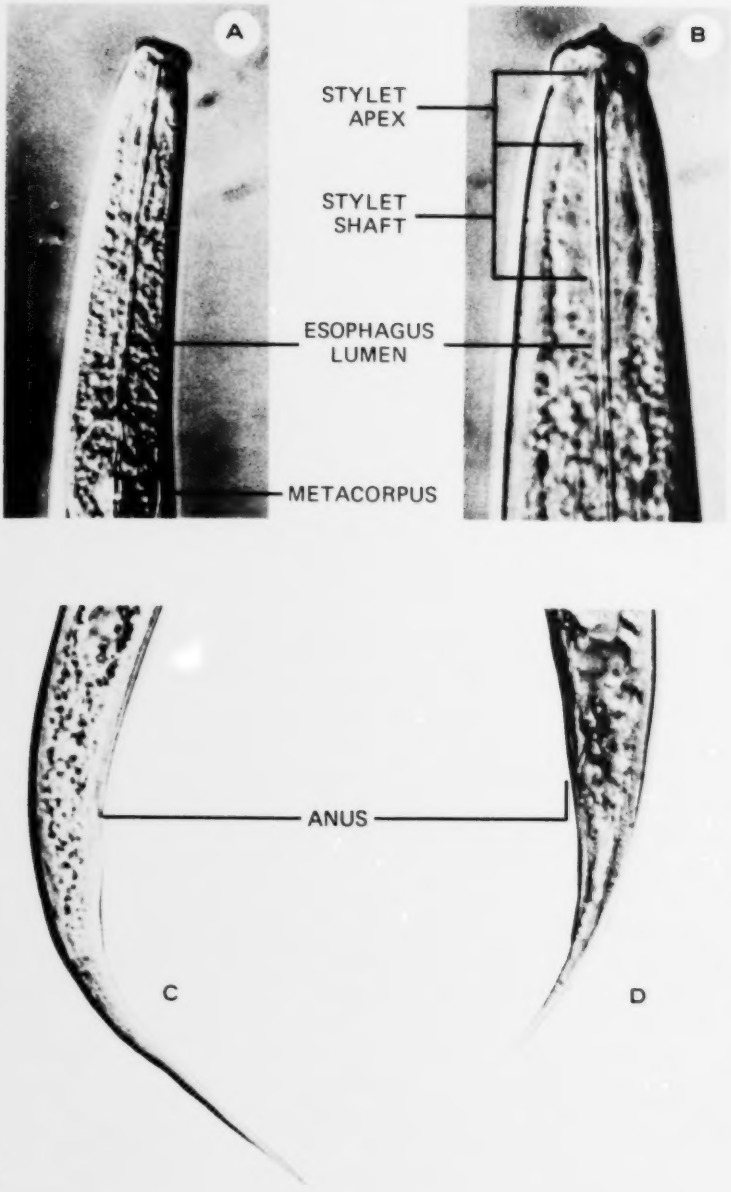


Fig. 74. *Seinura*. *A*, Head end. *B*, Stylet illustrating the form and parts characteristic of these and many other species of aphelenchids. *C* and *D*, Female tails of 2 species. The filiform shape of the female and male tails readily separates these species from those of other genera. All species are predators of other nematodes and are not known to feed on plants or fungi.

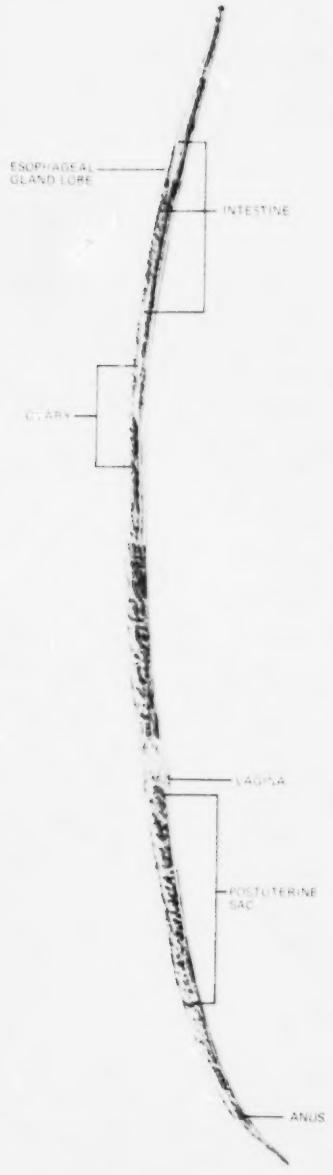



Fig. 75. Adult female of *Aphelenchoides ritzemabosi*, chrysanthemum foliar nematodes, illustrating the body form typical for members of this genus. Some of the species of *Aphelenchoides*, the bud and leaf nematodes, are important plant parasites. Because they feed on the aboveground parts of plants, the disease symptoms are more conspicuous and diagnostic than with root feeders. Most species of *Aphelenchoides*, however, are mycophagus and feed on fungi.

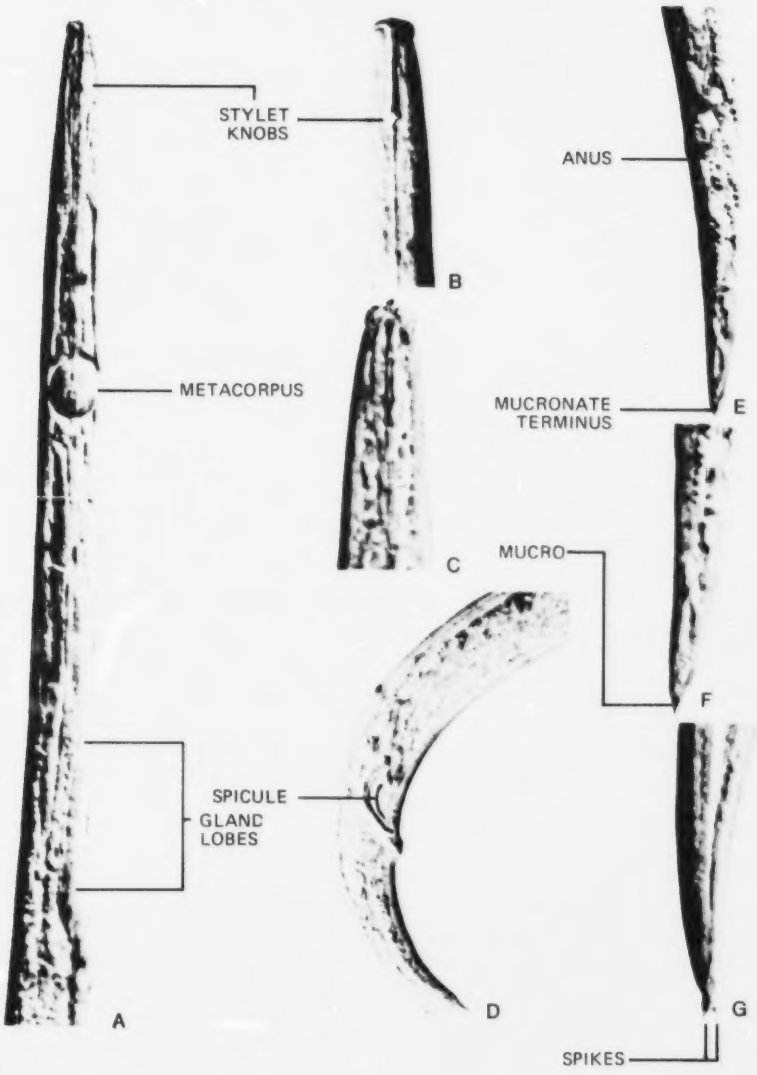


Fig. 76. *Aphelenchoides fragariae*, a bud and leaf nematode. *A*, Head and esophageal region, typical of the genus. *B*, Head and stylet enlarged. *C*, Head and stylet of a nonplant-parasitic species of *Aphelenchoides*. In species of *Aphelenchoides*, the stylet may have small knobs (*A*, *B*) or basal thickenings (*C*) or it may be without knobs or thickenings as in Figs. 42*D*, *E*; 73*B*, *C*; 74*A*, *B*; 78*A*. *D*, Male tail. Note the distinctive shape (rose thorn) of the aphelenchid spicules compared to the tylenchids (*see* Figs. 20*C*, *E*; 49; 50; 67*C*), the lack of a gubernaculum and a bursa, and the mucronate tail terminus. *E*, Adult female tail. *F*, Enlargement of the tail terminus showing the diagnostic single mucro of this species. *G*, Female tail terminus of *A. ritzemabosi*, the chrysanthemum foliar nematode, a closely related species that illustrates diagnostic differences in mucro shape. In this species, by contrast to other bud and leaf nematodes, the mucronated tail terminus has 4 fine spikes, 2 of which are visible in the photograph.

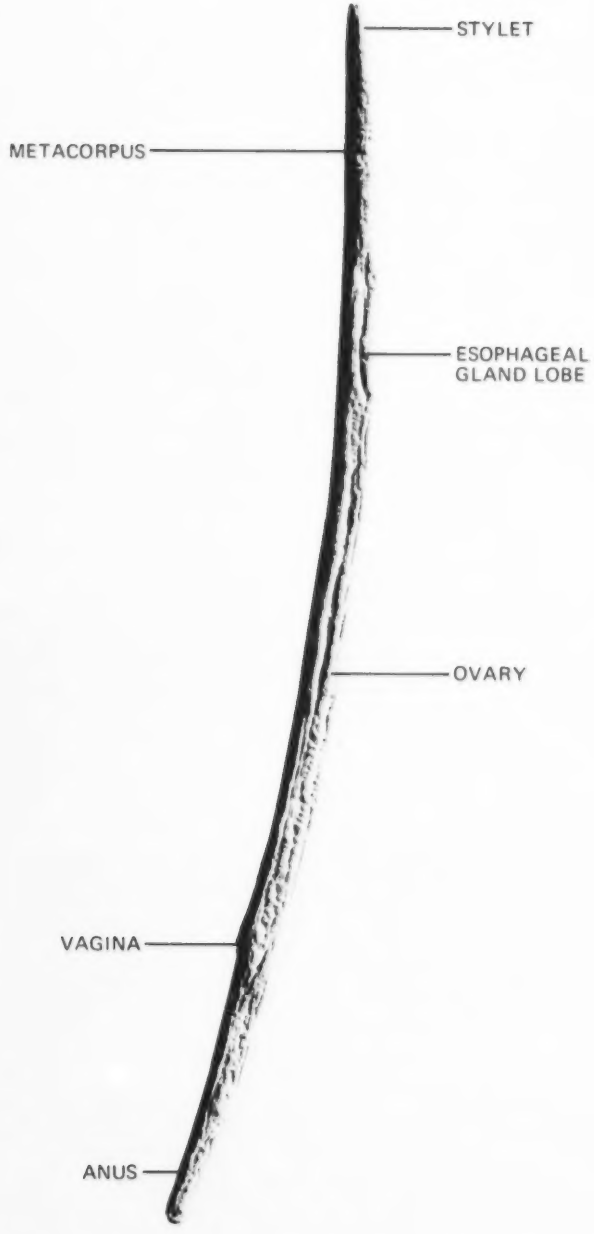


Fig. 77. *Aphelenchus avenae*, illustrating the characteristic body form of the genus. This species is one of the most common inhabitants of Canadian soils. It feeds mainly on fungi, but has been observed to feed also on root hairs and mycorrhizae.

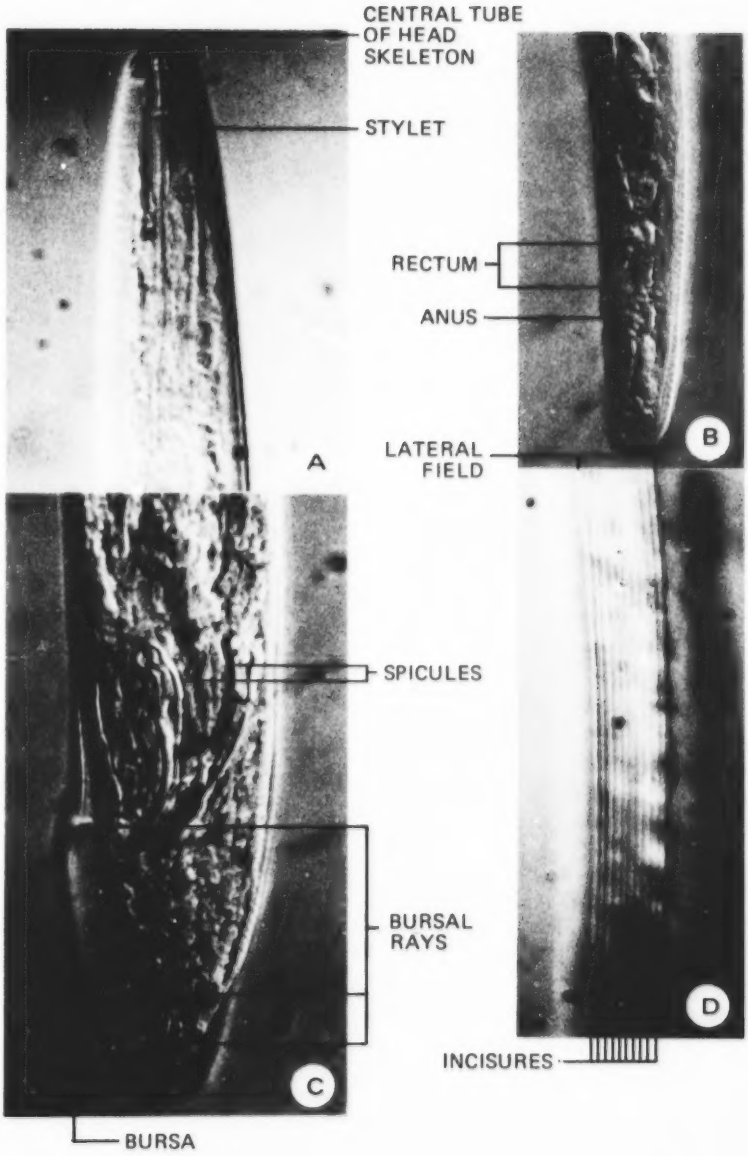


Fig. 78. *Aphelenchus* sp. *A*, Head end. The stylet always lacks knobs. Note the prominence of the central tube of the head skeleton. *B*, Representative tail shape (cylindrical) of the genus. *C*, Male tail. Males for these parthenogenetic species are rare and are not required for reproduction. Males are distinctive from all other plant-parasitic species by having a bursa with long sensory papillae or bursal rays. *D*, Lateral field of *A. avenae* with 10 incisures showing. With few exceptions most species have 8 to 12 incisures.

Fig. 79. *A*, Esophagus of a free-living dorylaimid species representative of the plant-parasitic members (Longidoridae, Fig. 80*A*). Note the narrow corpus, which lacks a metacorpus, and the large, muscular basal bulb containing gland cells (not evident) that exit through short ducts, usually contained within the basal bulb. *B* and *C*, A lateral and en face view of the head. In this large order of terrestrial and freshwater nematodes, the amphid apertures are posterior to the head. The large amphid pouches (*see* Fig. 85*B*, *C*) containing numerous nerve endings are a conspicuous feature of the amphidial nerves in the Dorylaimida. *D*, Ventral view of head showing the parts of the dorylaimid odontostyle, comprising the apex and extension, or shaft. Note the large, slit-like amphid apertures below the head (some of the amphid contents have exuded as a result of killing by heat). *E*, Representative male tail of dorylaimid species showing the characteristically large spicules and the often paired genital papillae. Although the dorylaimid plant parasites (Longidoridae, Trichodoridae) are less common than the Tylenchidae, they are unique in being able to transmit plant viruses.

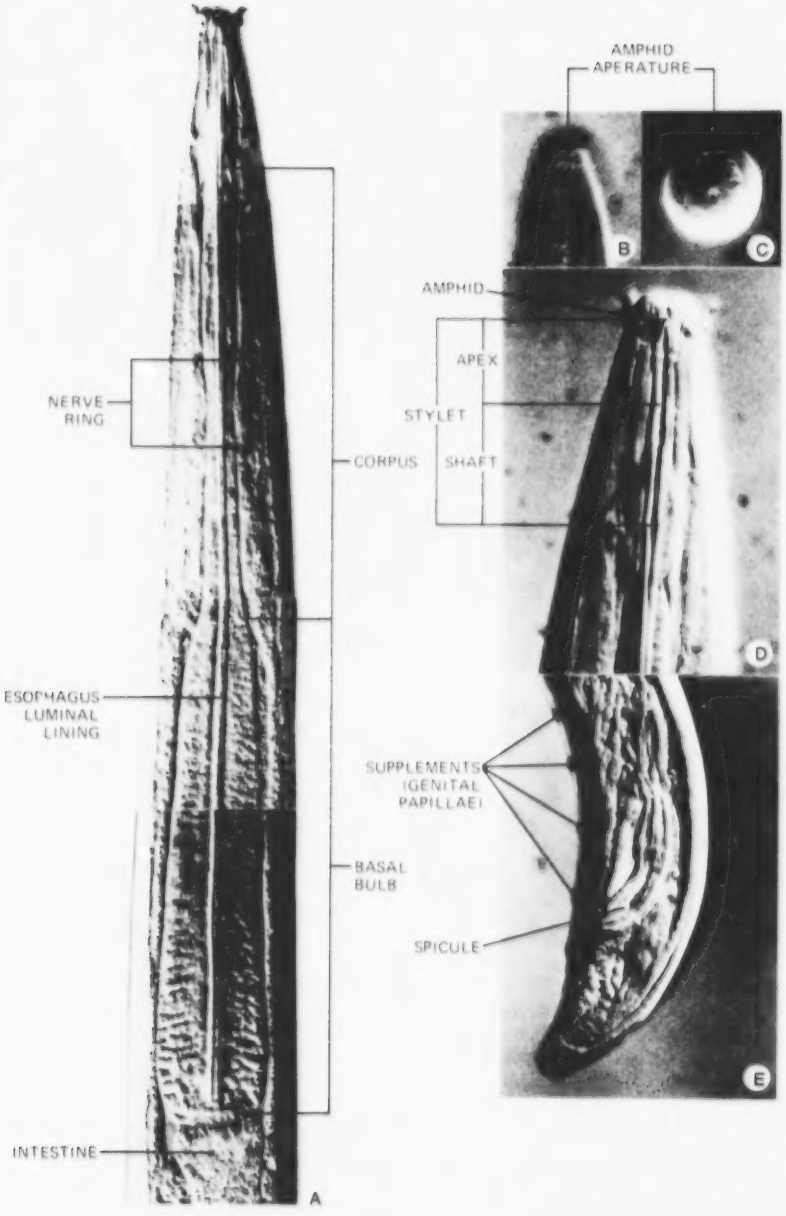
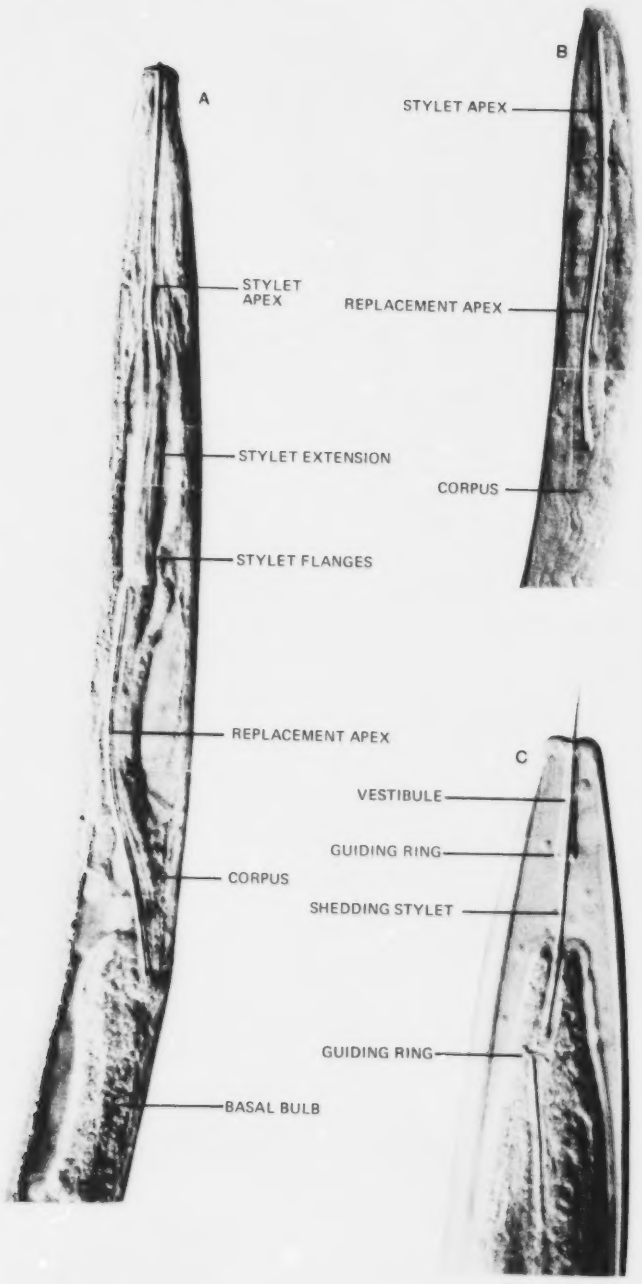

AMPHID
APERATURE
B
C
AMPHID
APEX
STYLET
SHAFT
NERVE
RING
CORPUS
D
ESOPHAGUS
LUMINAL
LINING
SUPPLEMENTS
(GENITAL
PAPILLAE)
BASAL
BULB
SPICULE
E
INTESTINE
A

Fig. 80. Development of the odontostyle of *Xiphinema*, the dagger nematodes. By contrast to the stomatostyle and onchiostyle, the apex of the odontostyle is formed in the anterior portion of the basal bulb following each molt, at the onset of each of the 4 developmental stages. Toward growth completion of each of the 4 stages, the stylet apex gradually moves anteriorly through the tissue of the narrow corpus (*A*). Before molting, the extension of the old stylet disappears and the void becomes occupied by the new stylet apex (*B*). During each molt, the old stylet apex is shed with the cuticle and is replaced by the newly formed apex (*C*) and a new extension is formed. Immatures (larvae) of the species with odontostyles are readily recognizable by the presence of a second stylet apex within the esophagus (*A*, *B*). In those species with an onchiostyle, such as the Trichodoridae, the stylet apex is formed in close proximity to the existing apex. Most of the plant-parasitic nematodes have a stomatostyle (Tylenchina and Aphelenchina) in which the apex is formed "in place" of the molting apex and does not move into position as is the case with odontostyles and onchiostyles.


A
STYLET APEX
STYLET EXTENSION
STYLET FLANGES
REPLACEMENT APEX
CORPUS
BASAL BULB
B
STYLET APEX
REPLACEMENT APEX
CORPUS
C
VESTIBULE
GUIDING RING
SHEDDING STYLET
GUIDING RING

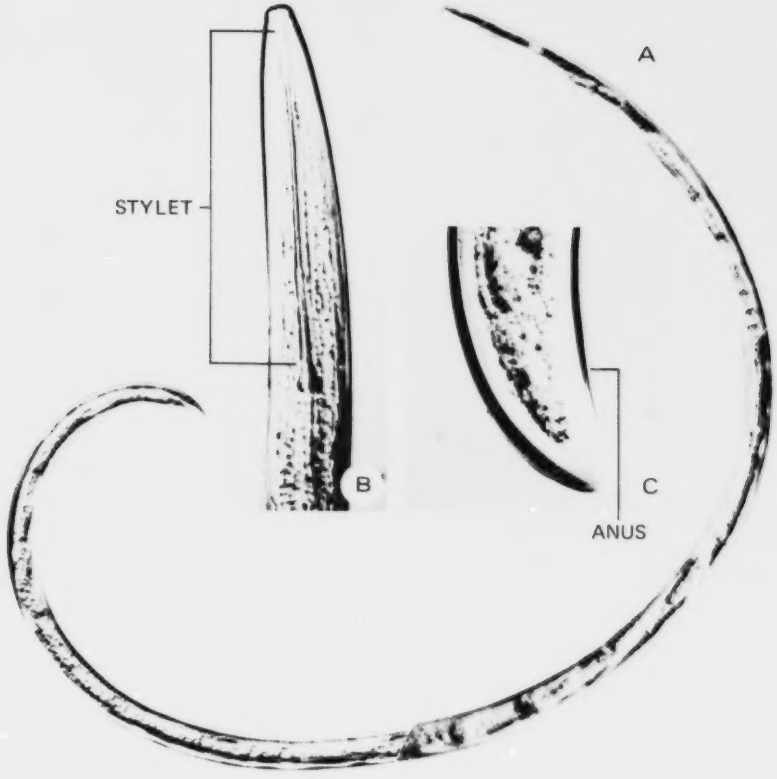


Fig. 81. *A*, Adult female of *Xiphinema americanum* showing the usual body shape and proportions of relaxed, dead specimens. *B*, Head end containing a fully developed odontostyle, characteristic of the genus. *C*, Female tail having the diagnostic shape (convex-conoid) of *X. americanum*, a commonly occurring species of dagger nematode in Canada.

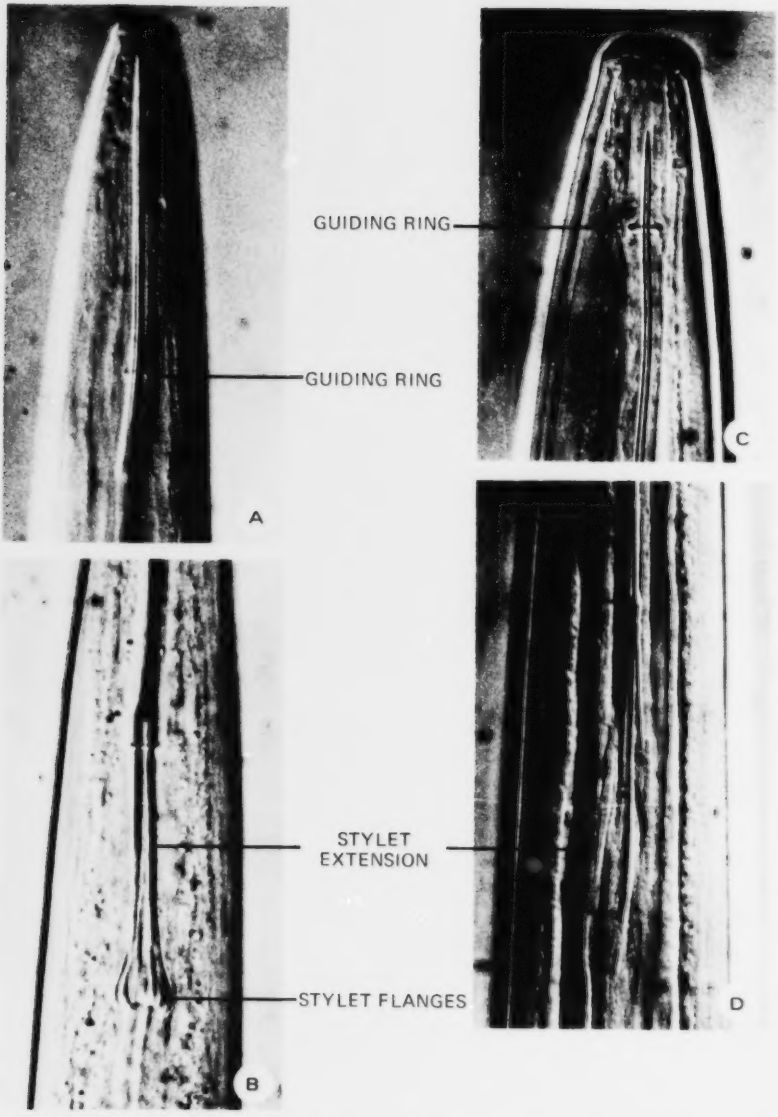


Fig. 82. Anterior body and stylets of the dorylaimid plant parasities (Longidoridae) showing their main differential characteristics. *A*, Stylet apex and guiding ring of *Xiphinema*. *B*, Stylet extension of *Xiphinema* characterized by having flanges or knobs. *C*, *Longidorus*, the needle nematodes, showing the stylet apex and guiding ring, which is significantly more anterior than in *Xiphinema* spp. *D*, Stylet extension of *Longidorus*, which is distinctive by the absence of flanges or knobs.

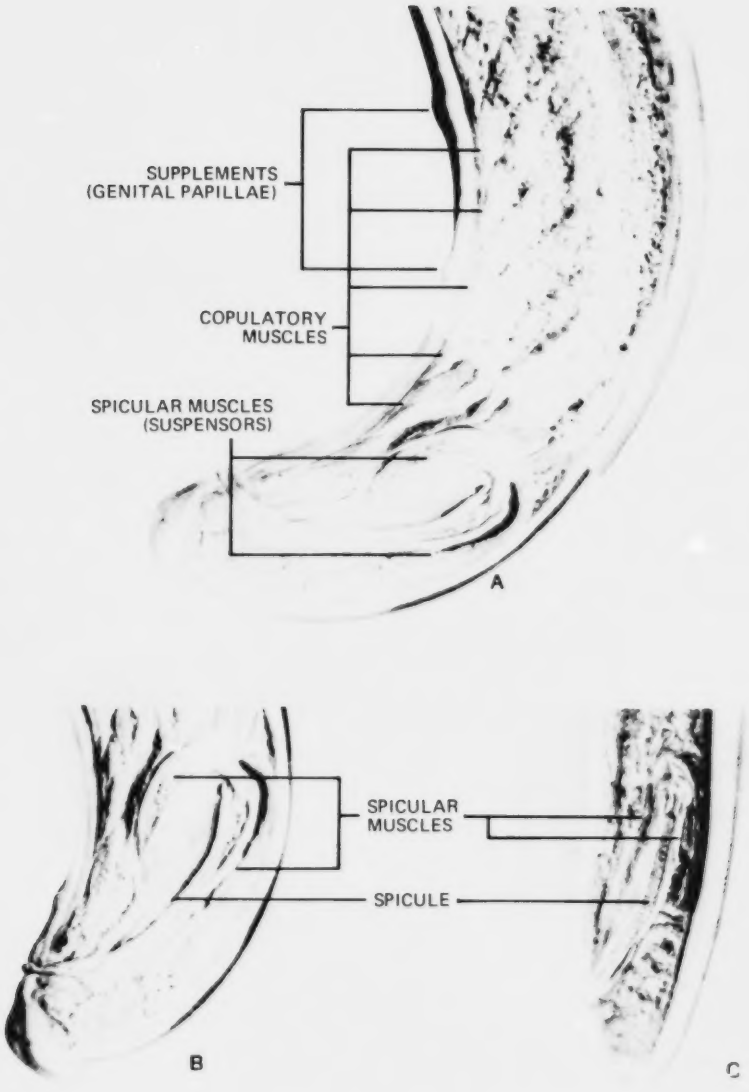


Fig. 83. Diagnostic differences in the male copulatory organs of species of *Trichodorus* (*A*, *B*) and *Paratrichodorus* (*C*). *A* and *B*, Male tails of *Trichodorus*. Note the large, circular suspensor muscles controlling movement of the spicules, the genital papillae, and the heavy bands of copulatory muscles along the ventral body wall anterior to the spicules (*A*). *C*, Male tail of *Paratrichodorus*. Species of this genus differ by having weakly developed, linear suspensor muscles; lacking genital papillae and copulatory muscles anterior to the spicules; more linear spicules; and a thicker, expanded body cuticle.

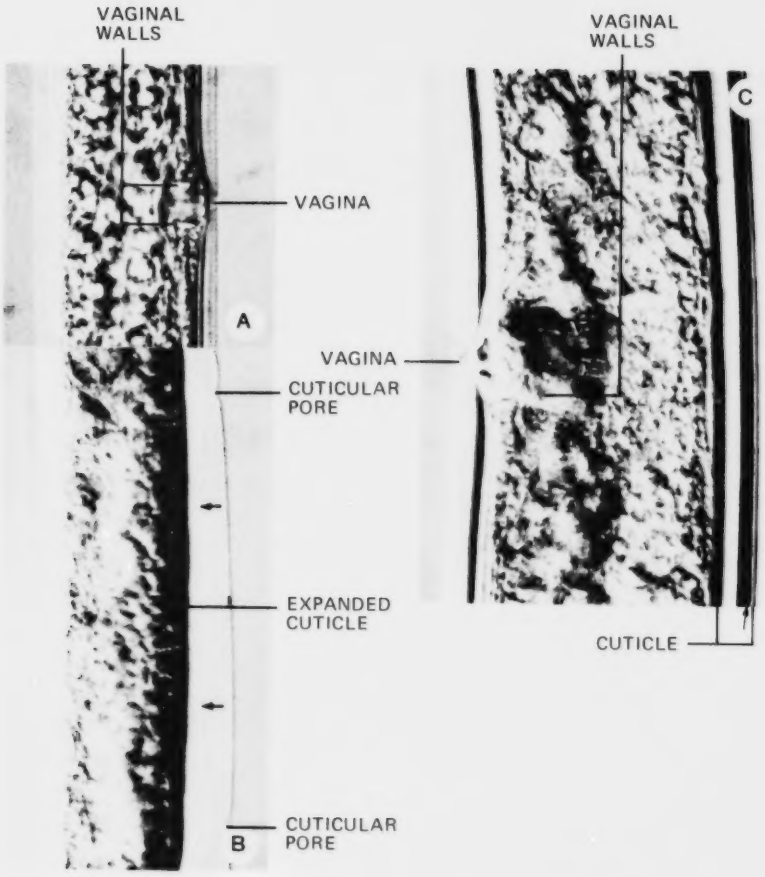


Fig. 84. Diagnostic differences in the female vagina and body cuticle of species of *Paratrichodorus* (*A*, *B*) and *Trichodorus* (*C*). *A*, Vagina of *Paratrichodorus*. Note the small fine features, particularly the thin vaginal walls. *B*, Longitudinal view at midbody of *Paratrichodorus* showing the thickened, expanded cuticle that is characteristic of heat-killed and preserved specimens of this genus. Note the conspicuous inner layer of the cuticle (arrows) and the cuticular pores common to the Dorylaimida. *C*, Vagina of *Trichodorus*, which is distinguished from species of *Paratrichodorus* by being larger and better developed and having markedly thicker walls. The cuticle of the species of *Trichodorus* does not expand after death.

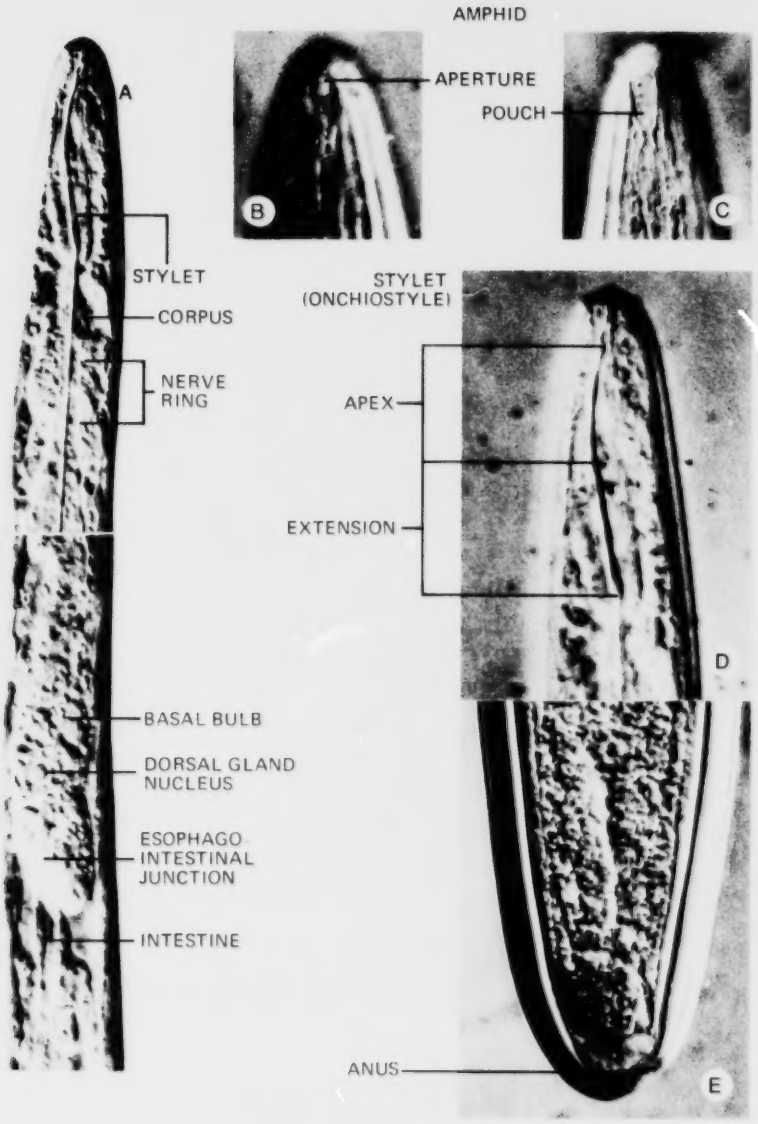


Fig. 85. *A*, Esophagus of a species of *Paratrichodorus*. In most of the species the subventral glands overlap the intestine (as shown) in short lobes, whereas in *Trichodorus*, the glands always appose the intestine. *B* and *C*, Lateral view of a sublabial amphid in the Trichodoridae showing the elongated aperture (*B*) and the large amphid pouch (*C*) characteristic of the Dorylaimida. *D*, Typical structure and shape of the stylet (onchiostyle) of species of Trichodoridae, the stubby root nematodes. *E*, The short, broadly rounded tail of females is a family characteristic. In these species, the anus is at the tail terminus. Like the Longidoridae, these species are ectoparasites and have been known to transmit viruses, which increases their economic importance.

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Glossary

adanal In close proximity to the anus, particularly with reference to accessory male copulatory structures such as the bursa (Fig. 14*D*).

adult A sexually mature female or male. That stage (5th) following the 4th and final molt when the reproductive system is fully developed. Adult females are recognizable by the presence of a vulva and vagina and the males by spicules, gubernaculum, and when present, the bursa. The identifying characteristics of nematodes are based largely on the adults.

amalgamated Usually with reference to the lips when not discernibly separated from each other in a side view.

ambifenestrate In cyst nematodes, semifenestra (half-windows) formed along other sides of the vulva (Fig. 66*D*) but not surrounding the vulva. *See* circumfenestrate.

amphid One of a pair of lateral chemoreceptor sense organs associated with the central nervous system that open on or near the head (Figs. 35, 53*A*, 65*C*, 67*A*). The amphid comprises the amphid aperture and the receptor organ (amphid pouch or sensillar pouch), which contains nerve endings or sensilla. The amphid pouches are a conspicuous feature of the Dorylaimida (Fig. 85*C*), but are obscure in the Tylenchida.

amphidelphic Female having opposed ovaries, usually one anteriad and one posteriad from the vagina (Fig. 45). The vagina is usually located near midbody in amphidelphic species (Figs. 59, 60).

ampulla Expanded portion of the esophageal gland extensions at the terminal duct (duct orifice), which serves as a reservoir for the accumulation of salivary secretions (Fig. 71*A*).

annule Small convex unit of body cuticle set off by transverse striae (Fig. 3*B*) dividing the surface of the cuticle into rings or annules (Figs. 3, 21*C*, 22, 53*A*). The size and number of body annules are diagnostic characteristics. In most species of plant-parasitic nematodes, the annules are less than 2 μm wide (Fig. 2).

anus In females, ventral terminal opening (Fig. 21*C*) of the intestine, preceded by the rectum (Figs. 42*F*, 78*B*); the cloacal opening in males

(Fig. 50*A*). The anus marks the anterior limit of the tail (Figs. 33; 34*A*; 47*B*, *D*, *E*). It is conspicuous in most species except in the ring nematodes.

apex Anterior subulate part of the stylet (Figs. 24, 53*C*, 56*E*).

apposed Transverse junction between tissues such as occurs between the esophageal gland bulb and intestine in some species (Figs. 2; 12*D*, *E*; 15).

arcuate Curved ventrally (Figs. 16, 25*A*, 29*A*, 33, 43).

axial Relative to the central axis of a cylindrical body or organ such as the stomatostyle (Fig. 24) and esophageal lumen (Fig. 79*A*).

awl nematodes Species of *Dolichodorus* (Figs. 43, 44).

basal esophageal bulb (*also* basal bulb) Expanded posterior end of the esophagus containing the salivary glands (Figs. 2, 16, 79*A*). The basal bulb may be composed of glandular tissue (Tylenchida) or may be largely muscular (Longidoridae).

basal ring Posterior portion of the outer margin of the head skeleton, which extends into the body cavity and serves as attachment points for the somatic and stylet musculature (Figs. 55*A*, *E*; 56*D*).

bifurcate Divided into two parts, particularly with reference to the stylet knobs (Fig. 10*B*).

body That portion of the nematode between the esophagus and anus.

body wall The exterior covering of a nematode comprising the cuticle (exoskeleton), hypodermis (epidermis), and somatic muscles (Figs. 3*B*, 5).

bud and leaf nematodes Plant-parasitic species of the genus *Aphelenchoides* (Figs. 75, 76).

bulb and stem nematode The plant-parasitic species, *Ditylenchus dipsaci*.

bursa (*also* ala) Extensions or flaps of cuticle at the lateroventral sides of the male gonopore, which are used for clasping or orientating during copulation (Figs. 11*B*; 44*E*; 49*A*, *B*).

central tube The sclerotized cylindrical axis of the head skeleton through which the stylet extends during feeding (Figs. 47*A*, 55*C*, 73*C*, 78*A*).

circumfenestrate In cyst nematodes, when the fenestra surrounds the vulva and, in *Punctodera*, when the fenestra surrounds the anus (Figs. 68, 69, 70).

columella (*also* crustaformaria) A structural unit of the female gonad, anterior to the uterus proper, composed of columns of cells (Fig. 36*C*, *D*). The arrangement and number of cells are diagnostic. A columella of 4 columns of cells is termed a quadricolumella (Fig. 36*D*) and a columella of 3 columns of cells is a tricolumella.

continuous Uninterrupted, particularly with reference to the head and neck (Figs. 10*A*, *B*; 15*B*; 16) when contrasted with species with a set-off head (Figs. 44*C*, 47*A*).

copulatory muscles Heavy, oblique bands of muscles extending from the subventral to the lateral body wall in the posterior end of males, anterior to the cloacal opening (Fig. 83*A*).

corpus The anterior, predominantly muscular part(s) of the esophagus. *See* procorpus; metacorpus.

cuticle The outermost noncellular covering (exoskeleton) of nematodes, which is deposited by the hypodermis (epidermis). The cuticle of nematodes comprises a variable number of layers and zones (Fig. 3), which influences its permeability. Cuticular markings (such as annules, sculpturing, and perineal and cyst wall patterns) are important diagnostic characteristics.

cuticularized An arbitrary term for thickened structures derived from the cuticle such as the walls of the vagina (Fig. 84*A*, *C*) and the vestibule extension (Figs. 4*C*, 56*F*).

cuticular pores Minute pores opening at the surface of the cuticle, a usual feature of the dorylaimids (Fig. 84*B*).

cyst A white female (Fig. 66*C*) of the cyst-forming nematodes in which the cuticle has hardened and changed into a cyst (Figs. 66*B*, 68*A*, 70*A*) but it retains its typical female form. The protective, brownish cyst sustains the viability of the eggs for long periods in the soil. Consequently crop rotation of at least 4-year intervals remains one of the most satisfactory control measures.

cyst nematodes Sedentary endoparasitic species of the family Heteroderidae, characterized by the transformation of a swollen female into a cyst (Fig. 66*A*, *C*).

dagger nematodes Plant-parasitic species belonging to the genus *Xiphinema* (Fig. 81).

didelphic Broadly defined, a female having 2 ovaries (Figs. 43, 45, 59, 60). A didelphic, amphidelphic female has 2 gonads that are opposed. *See* amphidelphic.

digitate Finger-like in shape or divided into finger-like processes.

distal Remote from the point of origin or attachment.

dorsal arch (*also* posterior cuticular patterns) Pattern of cuticular striations in the perineum of adult *Meloidogyne* females dorsad of the anus and lateral fields (Fig. 62). In these spherical females the anus is dorsad to the vulva; the tail is usually obscure and unrecognizable.

dorsal esophageal gland One of usually 3 glands of the basal esophageal bulb located dorsally in the body, as indicated by usually having a larger and more anterior nucleus than the subventral glands (Figs. 12*C*, *D*; 51*A*, *B*).

dorsal esophageal gland orifice (*also* terminal duct) A cuticularized, short tube at the exit of the dorsal gland leading to the lumen of the esophagus (Fig. 64*D*). In species of the Tylenchida the terminal duct is well anterior to the glands, either in the metacorpus (Fig. 71*A*) or procorpus (Figs. 2, 4*C*, 13*A*).

dorylaimida A large group of mainly free-living terrestrial and freshwater species having an odontostyle or onchiostyle. The relatively few plant-parasitic species, as compared to the Tylenchida, are of particular interest because of their ability to transmit plant viruses.

ectoparasite An obligate plant-parasitic nematode that feeds (grazes) externally and does not penetrate the host tissue. *See* endoparasite.

egg mass A large cluster of eggs contained in a gelatinous matrix deposited by female root-knot nematodes (Fig. 64*A*) and some *Heterodera* spp. Like the cyst, the gelatinous covering affords a degree of protection for the eggs from adverse conditions and parasites.

endoparasite An obligate plant-parasitic nematode that penetrates and feeds within plant tissue (Figs. 7, 8). *See* ectoparasite.

esophagus (*also* pharynx) In nematological nomenclature, the component muscular and glandular portions of the digestive tract, precluding the stylet and intestine (Figs. 2, 79*A*). Measurements of the esophagus, however, are taken from the head tip to the esophagointestinal valve or terminus of the glands. The great diversity in nematode esophagi is of primary importance in the classification of nematodes. The esophagus of members of the order Tylenchida comprises a muscular procorpus, metacorpus, isthmus, and a glandular basal bulb (*see* Figs. 15, 16). The esophagus of dorylaimid plant parasites comprises a corpus and a muscular (Fig. 79*A*) or glandular (Fig. 85*A*) basal bulb. In cross section, the esophagus is divisible into 3 sectors, a dorsal and 2 subventral (Fig. 71*B*). The glands contained within these sectors are named accordingly. *See* dorsal esophageal gland; subventral esophageal glands.

esophagus bulb (*also* basal bulb) The posteriormost part of the esophagus, immediately adjacent to the intestine (Fig. 15).

esophageal glands Unicellular salivary glands of various size that are contained in or comprise the basal esophageal bulb (Fig. 51).

esophagointestinal valve A transitional cellular junction joining the esophagus and intestine (Figs. 12*D*, *E*; 39*B*, *C*; 44*A*). The structure and position of this valve are diagnostically important, particularly in species having glands that overlap the intestine (Figs. 9*B*; 51*A*; 58*E*, *F*).

excretory duct A cuticularized tube leading anteriorly from the renette (Figs. 2, 13*E*, 52*B*) and opening ventromedially on the body. Differences in refractiveness of the duct between species may sometimes be diagnostic.

excretory pore The ventromedial opening of the excretory system (pore, duct, and renette; Fig. 13*D*, *E*) usually at the posterior half of the esophagus (Figs. 2, 19*F*). The position of the excretory pore, from the head end or in relation to parts of the esophagus, is a diagnostic character.

fenestra In a cyst, a thin membranous area surrounding or on either side of the vulva (and anus in *Punctodera*). The fenestra exists during cyst formation (Figs. 66*D*; 68*B*, *D*; 69; 70*B*, *C*) and deteriorates in the mature cyst to form an escape hole (Fig. 68*B*) for the hatching larvae.

flanges Posteriorly sloping thickenings or knobs at the base of the odontostyle extension in *Xiphinema* (Figs. 80*A*, 82*B*).

gall Isolated or aggregated knots or swellings in plant tissue, particularly with reference to the roots (Fig. 64*A*, *B*). A hyperplastic reaction of plant tissue to feeding of plant-parasitic nematodes, particularly symptomatic of the root-knot species.

ganglion Discrete group of nerve cells, particularly numerous in the esophageal region (Fig. 10*A*).

gelatinous matrix An external glandular substance secreted by the mature female of root-knot nematodes and some species of *Heterodera* into which the eggs are embedded or deposited (Fig. 64*A*).

genital papillae (*also* supplements) Sensory nerve terminations of various size, form, and arrangement on or near the male tail. They are particularly prominent and diagnostic in males of the Dorylaimida (Figs. 79*E*, 83*A*).

germinal cells Products of the germinal primordium; the oocytes and oogonia (Figs. 36*A*; 37*A*, *B*) that are contained within the mature ovary, or the spermatogonia and spermatocytes of the testis.

gonad The distal portion of the reproductive system producing and containing the germinal cells; the ovary (Fig. 37*A*, *B*) or testis.

gonopore External, ventromedian opening of the male or female reproductive system; the vulva (Figs. 16, 21*C*) or cloaca (Fig. 50*A*).

gubernaculum A short, sclerotized trough-shaped reinforcement of the dorsal wall of the spicular sheath, lying in close proximity to the distal portion of the spicules in males (Figs. 49*D*; 50*A*, *B*). The presence, or absence, size and form of the gubernaculum are diagnostic.

guiding ring Ringed thickening, junction, or fold of cuticle ensheathing the stylet. A guiding ring is particularly prominent and diagnostic in the dorylaimids (Fig. 82*A*, *C*).

head The anteriormost discrete portion of the nematode, comprising the lips and sensory organs, oral opening, and supporting head skeleton (Figs. 35*A*, 53*A*, 55, 56). When set off, the head is clearly demarcated by a constriction (Figs. 40*H*; 44*A*, *C*; 55*A*). When continuous with the body (Fig. 56*E*, *F*, *G*) or when the limits of the head are obscure (Figs. 24, 46*B*, 53*D*), it is delineated by the septum of the head skeleton, precluding the basal ring (Fig. 55*E*). Form of the head, arrangement of the lips, and character of the annulation (if present) are important identification aids.

head cap A large, elevated dorsoventral segment at the head apex formed by fusion of the subdorsal and subventral lips. The head cap is particularly prominent in males of some Heteroderidae (Fig. 65*A*, *B*, *C*).

head end A general term for the anterior portion of the nematode, which includes the head and all or part of the esophagus.

head skeleton (*also* cephalic head framework) The supporting, sclerotized frame of the head including the axial central tube (vestibule), radial lamina (blades), septum, and basal ring (Fig. 55). Differences in thickness (refractiveness) of the head skeleton are useful diagnostic features of plant-parasitic species (Figs. 34*B*, *C*, *D*, *E*; 55).

hemizonid An oval or elliptical subcuticular cavity, usually immediately anterior to the excretory pore, formed by large, paired lateroventral commissures joining nerves of the central nervous system (Fig. 19*D*, *E*). Its position in relation to the excretory pore or esophagus parts may be diagnostic.

hypodermis A thin cellular layer (the epidermis) between the cuticle and somatic muscles (Fig. 5) that extends into the pseudocoel between muscle fields and forms chords. The hypodermis produces the cuticle.

immature (*also* juveniie, larva) Any of the developmental stages preceding the adult (Fig. 1).

incisures The longitudinal striations present in and bordering the lateral field (Figs. 40*D*, 48, 78*D*). Differences in incisure number between genera, as well as species, are useful identification aids.

infective larva The earliest immature stage of development capable of attacking and infecting a host plant; usually the 2nd stage female larva (Fig. 63*A*, *D*).

intestine The cylindrical, cellular or syncytial portion of the digestive tract between the esophagus and rectum (Figs. 10*D*, 16, 52), bounded externally by epithelium and internally by lumenal cuticle of various thicknesses and forms. The cytoplasm of the intestine is typically opaque because of the many storage globules.

isthmus In the Tylenchida, the narrow, muscular part of the esophagus joining the metacorpus and basal bulb (Figs. 2, 15, 21). The lumen is triradiate (Fig. 4*E*) in contrast with the cylindrical lumen of the procorpus (Fig. 4*B*).

labial disk In some species, a circular elevation of cuticle surrounding the oral opening that interrupts the rounded contour of the head (Fig. 46*D*, *E*).

labial plates Vertical division of the anteriormost head annule into plate-like sections in some species of Criconematidae (Fig. 27*A*, *D*).

lamina *See* radial lamina.

lance nematodes Species of the genus *Hoplolaimus* (Figs. 7, 55).

larva (*also* immature, juvenile) Any young postembryonic stage of development preceding the 4th and final molt; characterized most conspicuously by the absence of a vagina in females and spicules in males.

lateral field Lateral, longitudinal band of modified cuticle usually marked by incisures and interrupting the transverse annulation (Figs. 48; 61*E*, *F*; 78*D*). Prominent in the Tylenchida, the lateral field originates in the esophageal region and terminates on the tail, usually near or at the terminus (Figs. 47*F*, 57*B*). The thickening of the cuticle at the lateral fields (Fig. 48*E*) provides additional rigidity and restricts body movement in nematodes to a dorsoventral plane.

liplets (*also* pseudolips) Small, reduced lips restricted to the apex of the head; a feature of some ring nematodes (Fig. 26*A*, *B*).

lips (*also* labia) External division of the head cuticle into 6 basic units (or modifications thereof), each bearing a complement of sensory papillae. There are typically 2 subdorsal, 2 subventral, and 2 lateral lips (Fig. 35*A*) that internally are divided by the radial lamina of the head skeleton (Figs. 12*A*, 55).

lumen Central, tubular cavity of an organ or duct through which nutrient or glandular suspensions pass.

lumenal lining The inner lining of an organ that borders the lumen (Figs. 2, 79*A*); particularly with reference to the esophagus. The lumenal lining of the esophagus differs diagnostically and phylogenetically in morphology and function in nematodes.

metacorpal valve (*also* valvular apparatus) An expanded portion of the triradiate lumen at the center of the metacorpus that has a greatly thickened lumenal lining to which massive radial muscles are attached (Fig. 4*A*, *D*). The metacorpal valve functions as a pump during feeding to withdraw the liquified cytoplasm from the food cell.

metacorpus (*also* median bulb) The expanded, usually strongly muscular portion of the esophagus near its middle; at the base of the procorpus and preceding the isthmus in members of the Tylenchida (Figs. 2, 15, 51). Differences in size and development of the metacorpus, with or without a valvular apparatus, are important diagnostic features of the higher nematode taxa (Figs. 9*C*, 10*A*, 16, 73*A*).

migratory endoparasite A plant-parasitic nematode that invades and moves through plant tissue as it feeds and reproduces (Figs. 7, 8).

monodelphic Broadly defined, a female having 1 gonad. A monodelphic, prodelphic female has 1 ovary directed anterior to the vagina (Figs. 16, 17, 33, 75, 77).

mucronate (*also* spicate) Abrupt tapering of the tail terminus to a sharp point or spine (Fig. 76*D*, *E*, *F*, *G*).

mucro A small pointed ending on a tail terminus.

muscle field One of 4 symmetrical sectors of 2 or more somatic muscle cells (Fig. 5) separated by chords of hypodermal tissue containing nuclei of the hypodermis, somatic nerves, and sometimes gland cells.

neck That portion of the nematode body from the base of the head to the termination of the esophagus. Also, in some species of ring nematodes, the narrow, posterior part of the head (Fig. 26*C*).

needle nematodes Species of the genus *Longidorus* (Dorylaimida: Longidoridae; Fig. 82*C*, *D*).

nerve ring A circumesophageal band of nervous tissue encircling the isthmus in the Tylenchida (Figs. 10*A*, 13, 51, 73) and the corpus in the Dorylaimida (Figs. 79*A*, 85*A*).

nematode A member of a large, diverse group of free-living and parasitic roundworms, phylum Nematoda. Nematodes have an external covering of cuticle and well-developed nervous, reproductive, and digestive systems, but they lack segmentation and a true coelom. They are vermiform in larval and most adult stages and typically move in a dorsoventral plane. There are about 2000 known species of plant-parasitic nematodes, about 10% of which occur in Canada.

odontostyle A type of stylet possessed by many of the free-living and plant-parasitic (Longidoridae) species of the Dorylaimida (Figs. 79*D*, 81*B*, 82). The stylet apex reforms during each of the larval stages in the anterior subventral sector of the esophageal bulb, moving progressively through the corpus to finally replace the apex shed during the molt (Fig. 80). The oblique orifice of the odontostyle is dorsal.

onchiostyle A type of stylet, characteristic of the Trichodoridae parasites, in which the new apex forms in close proximity to the side or base of the existing apex (Fig. 85*A*, *D*).

oocyte A cell in the ovary derived from the oogonia, which undergoes meiosis, giving rise to ova or eggs (Fig. 37*A*).

oogonia Germinal cells in the anterior of the ovary derived from a germinal primordium, which gives rise to the oocytes by mitotic division (Figs. 36*A*; 37*A*, *B*).

oral opening (*also* mouth) The external entrance on the head to the digestive tract (Figs. 53*A*; 67*A*, *B*) through which the stylet extends during feeding (Figs. 7*B*, 22*D*).

orifice An opening, particularly with reference to the exits of the esophageal salivary glands (Fig. 4*B*, *E*). *See* dorsal esophageal gland orifice; subventral esophageal gland orifice.

outstretched A linear, posteriad or anteriad ovary or testis (Figs. 37, 45); in contrast with one that is reflexed.

ovary (*also* gonad) The tubular distal part of the reproductive tract containing the germinal cells (oogonia and oocytes; Fig. 37), bounded by a thin, transparent epithelial layer.

overlapping Extending over or covering a part of; with particular reference to esophageal glands that extend posteriorly over the intestine and beyond the esophagointestinal valve (Fig. 51).

perineal Belonging to the perineum.

perineal tubercles Clusters of wart-like protuberances of cuticular origin in the perineum; characterizing the cyst nematode genus *Globodera* (Fig. 69*A*, *B*).

perineum Surface area between or in close proximity to the anus and vulva; of particular diagnostic value in the root-knot and cyst nematodes (Fig. 62).

perorial Around, enclosing, or surrounding the oral aperture.

perioral disk *See* labial disk.

phasmids Caudal chemosensory organs that open in each of the lateral fields, usually on or near the tail (Figs. 47*F*; 58*A*, *B*). The size and position of the phasmid pore are important diagnostic characteristics. The unusually large phasmids of some species are sometimes termed scutella (Fig. 58*C*, *D*).

pin nematodes Species of the genus *Paratylenchus* and *Gracilacus* (Figs. 16, 17).

posterior protuberance (*also* cone top, vulval cone) The cone-shaped projection on the posterior end of the cyst, characterizing some species of Heteroderidae, which bears the vulva and anus (Fig. 66*B*, *D*). Morphological features of the vulva, vagina, and anus of mature cysts and, to some extent, of white females form the basis for distinguishing the genera.

postuterine branch (*also* postuterine sac) A reduced, degenerate ovary, usually posteriad to the vulva, that is nonfunctional in gamete production (Fig. 11*D*), but may serve as a storage organ for sperm in some species (Fig. 75).

procorpus The anteriormost cylindrical part of the Tylenchida esophagus, between the stylet and metacorpus. The procorpus is distinctive because it has a thick circular lumenal lining (Figs. 2; 4*A*, *B*; 9*C*; 15; 16).

prodelphic Female with a single ovary anterior to the vulva (Figs. 16, 32). The vagina is usually located near the tail in prodelphic females (Figs. 21*C*, 25*F*, 26*D*, 27*D*, 34*A*).

protractor muscles Large contractile muscle elements attached to the stylet knobs or base and anteriorly to the body wall or head skeleton (Fig. 24). These muscles control the extension of the stylet, forcing the puncturing of the host cell.

pseudolips *See* liplets.

rachis An axial cylinder of matrix in the ovary around which multiple rows of germinal cells are laid down; particularly with reference to species of the seed gall nematode (Fig. 36*B*).

radial lamina Thin, sclerotized plates radiating from the central tube of the head skeleton dividing the head into usually 6 uniform sectors (Figs. 55*B*, *C*, *D*; 56*A*, *B*, *C*).

refractive General term for the nontransparent structures of nematodes such as the stylet, metacorpal valve, and storage globules of the intestine.

renette Ventral excretory gland cell(s).

ring nematodes Species of the family Criconematidae; a common name derived from the heavy body annulation (Figs. 5, 20).

root-knot nematodes The sedentary endoparasitic species of the genus *Meloidogyne* that produce the symptomatic galls on roots of many plants (Fig. 64).

root-lesion nematodes Migratory endoparasites of the genus *Pratylenchus*. Their feeding activities in root tissue often result in darkened lesions (Fig. 8).

reproductive system A male or female close-ended, self-contained tubular organ lying free in the pseudocoel and exiting through a gonopore on the ventral body surface. This tubular organ is used in reproduction. The diagnostic features of the female reproductive system are the ovary, spermatheca, columella, uterus, vagina, vulva, and postuterine branch (Figs. 11*C*, *D*; 16; 36*C*, *D*; 45). The sexual characteristics of the male are based largely on the accessory copulatory apparati, including the spicules, gubernaculum, bursa, and genital papillae.

saccate Sac-shaped or spheroid in form, such as the adult female root-knot nematode.

scales Thickened, retrorse modifications of the body annules arranged in uniform longitudinal rows in some species of the Criconematidae (Figs. 29, 30).

sclerotized (*also* sklerotized) A subjective term characterizing heavily thickened structures, in contrast with cuticularized, that are supportive such as the head skeleton, or movable such as the stylet, metacorpal valve, and spicules.

scutellum One of a pair of large caudal chemosensory organs opening in the lateral fields in some species of the Hoplolaimidae (Fig. 61*E*, *F*); a phasmid.

secretory granules Proteinaceous granules produced in the salivary (esophageal) glands, which are transported anteriorly to the gland ampullae where they break down, presumably releasing digestive enzymes that are injected into the food cell during feeding.

seed gall nematodes Fecund species of the genus *Anguina* and some related forms not known in Canada that attack the leaves and particularly flower buds of grasses and transform the seed into blackened galls

(cockles, purples, peppercorns) containing thousands of larvae. The wheat nematode, *A. tritici*, was the first plant-parasitic nematode recorded and was discovered by Needham in 1743. The species of this genus are unique in their ability to survive desiccation for periods of more than 30 years.

septum The transverse, foraminate basal plate of the head skeleton connecting the central tube and radial lamina anteriorly and the basal ring posteriorly (Fig. 55*A*, *E*).

sessile nematode A sedentary parasite in contrast to a migratory endoparasite; one that becomes permanently embedded wholly or in part in living host tissue (Figs. 64*A*, 66*C*).

set off Particularly with reference to the head when delimited from the body by a constriction (Figs. 44*C*, 47*A*, 55*A*, 73*B*).

shaft The cylindrical portion of the stylet (Figs. 24; 56*E*, *F*) continuous with the apex, but having a different origin and structure. *See also* odontostyle; onchiostyle.

shapes Body and structure shapes are important identification aids; the most common terms follow.

Body: saccate, spheroid (Figs. 64*C*, 66*B*, 68*A*, 70); linear (Fig. 1); arcuate (Figs. 43, 52, 63*D*); fusiform (Fig. 33); cylindrical (Figs. 1, 45).

Head: rounded (Figs. 46*D*, *E*, *F*; 56*A*, *B*, *C*, *D*, *E*, *F*), bulbous (Fig. 73); lobate (Figs. 34*B*, *C*, *D*, *E*; 44*C*); truncated (Figs. 18*C*, 46*B*, 56*G*).

Stylet knobs: rounded (Figs. 56*A*, *C*, *E*, *F*, *G*; 61*B*); indented (Figs. 28*A*, 61*D*); sloping (Fig. 46*F*); flange-like (Fig. 14*C*).

Esophageal bulb: pyriform (Fig. 12*E*); cylindrical (Figs. 12*D*, 79*A*); lobate, lobed (Figs. 51; 58*E*, *F*); bulboid, bulb-like (Figs. 2, 15).

Tail: filiform (Figs. 33; 74*C*, *D*); clavate (Figs. 42*C*, *G*; 46*C*); elongate-conoid (Figs. 19*A*, 47*E*, 54*A*); conoid (Figs. 21*C*; 34*A*; 54*B*, *C*); convex-conoid (Fig. 57*A*, *C*, *D*); cylindrical (Fig. 78*B*).

Tail terminus: broadly rounded (Fig. 57*E*, *F*); hemispherical (Figs. 25*F*, 57*G*, 78*B*); mucronate, spicate (Fig. 76*D*, *E*, *F*, *G*); digitate (Fig. 57*C*); clavate (Figs. 42*B*, *F*; 46*C*).

sheath nematodes Species of the genus *Hemicycliophora*; a common name derived from the feature of the double cuticle in adults (Fig. 23).

somatic muscles Long fusiform muscle cells arranged longitudinally along the body wall, which control the body movement (Figs. 3, 5).

spermatheca (*also* seminal receptacle) A saccate structural entity of the female reproductive tract serving as a receptacle for sperm (Fig. 38). Parthenogenetic species lacking males also may have a reduced or well-developed spermatheca (Fig. 38*E*), which is always devoid of sperm.

sphincter Constrictor ring of muscle maintaining closure of the vagina (Fig. 11*D*) and rectum.

spicular muscles Protractor and retractor muscles, circular or linear in shape, that attach to the protrusible spicules (Fig. 83).

spicules Tubular, sclerotized male organs of copulation, usually paired, located immediately dorsad to the cloaca (Figs. 49; 50; 67*C*, *D*, *E*; 79*E*; 83). The protrusible spicules function to dilate the vagina during copulation when the sperm is transported through the cloaca into the uterus. The dimensions and form of the spicules are important diagnostic characteristics.

spines Regular groupings of finger-like retrorse projections on the annules of some species of ring nematodes (Figs. 31, 32).

spiral nematodes Species of the genera of Hoplolaimidae that assume a spiral shape when killed (Figs. 59, 60).

stages The preadult increments in growth and in development of the reproductive system between molts in the development of the nematode (Fig. 1). Plant-parasitic nematodes advance through 4 stages of growth before attaining sexual maturity (adulthood).

striae The transverse or longitudinal creases on the surface of the body cuticle delineating the annules or plaques (Fig. 3).

stomatostyle A type of stylet in most plant-parasitic species (Tylenchida) in which the apex is formed axially in place of the cast apex during molting (Figs. 24, 56).

strengthening rings A series of 3 or more ringed thickenings of the stomatal cuticle ensheathing the stylet; a diagnostic feature of *Hexatylus* (Fig. 10*B*).

stubby root nematodes Species of the family Trichodoridae; a name derived from the typical symptoms produced by these species. Feeding at the apical meristems of roots arrests cell division and inhibits root elongation, causing the roots to have a stubby appearance.

stylet knobs Thickenings of various sizes and shapes (*see* shapes) at the base of the stylet; usually 3 (Fig. 55*F*), which serve as attachment points for the protractor muscles (Fig. 24).

stylet nematodes A common name for species of the family Tylenchorhynchidae.

stylet (*also* spear) A sclerotized, axial tube of cuticular origin in the head end, having a lumen continuous with the lumen of the esophagus (Figs. 24, 64*D*). The stylet is used in feeding to penetrate the walls of the food

cells (Figs. 7, 22*D*), to transport digestive enzymes into the host cell, and to withdraw the cell contents during ingestion when the metacorpal valve begins to function. The stylet is one of the most conspicuous and important of the diagnostic features of the plant parasites.

submedian lobes Term applied to the reduced, strongly modified, paired, dorsal and ventral lips of some species of ring nematodes (Figs. 27*A*; 30*A, B*).

subventral esophageal glands The salivary esophageal glands that are located in or comprise the 2 subventral sectors of the esophagus (Figs. 51*A, B*; 58*E*; 71*B*). *See also* esophagus.

subventral esophageal gland orifice (*also* terminal duct) A cuticularized, short tube at the exit of each of the 2 subventral glands in Tylenchida opening to the triradiate lumen of the esophagus (Figs. 4*A, E*; 71*A*). In species of the Tylenchida, the subventral gland orifices are always located in the metacorpus, immediately posterior to the metacorpal valve. In contrast with the dorsal gland terminal duct, the subventral orifices are inconspicuous and of no diagnostic value.

supplements (*also* genital papillae) Large, often paired papilliform sensory nerve terminations in the male ventral caudal areas; particularly characteristic of the Dorylaimida (Figs. 79*E*, 83*A*).

suspensors In a strict sense, the large circular muscles enclosing the distal part of the spicules; characteristic of males of the *Paratrichodorus* species (Fig. 83*A, B*).

tail Portion of the body in vermiform adults posterior to the anus (Figs. 16, 33, 45, 54, 57). In many species of ring nematodes the anus is obscure (Figs. 25*F*, 26*D*, 27*D*) and the tail is then generally considered as that portion of the body posterior to the vulva. In these species of ring nematodes, however, the position of the anus (Fig. 21*C*) in relation to the vulva and tail terminus remains of diagnostic value. The great diversity in tail shapes and dimensions in the plant-parasitic forms (*see* shapes) is an important diagnostic and identification aid.

terminal area A general term for the posterior ends of cysts containing the anus and vulva, particularly for cysts without a posterior protuberance (Figs. 68*A*, 70*A*).

terminal duct *See* dorsal esophageal gland orifice.

tubercles *See* perineal tubercles.

Tylenchida An order of about 1800 species of mostly obligate plant parasites of economic importance. Most plant-parasitic nematodes, as well as some mycophagous (some *Ditylenchus* spp.), predaceous (*Seinura*), and entomophilic species (some Aphelenchoididae), belong in this taxa.

vagina A short, cuticular-lined passage at the exit of the female reproductive tract connecting the uterus and vulva (Figs. 11*C*, *D*; 16; 26*D*). The vagina and gonopore, which form during the 4th and final molt, readily separate adults from larvae at low magnifications.

velum A thin, transparent extension of cuticle along the ventral surface of a spicule in males that is of particular diagnostic value in separating genera of the family Tylenchorhynchidae (Fig. 49*C*, *D*).

ventral The front side of the nematode on which the excretory system, reproductive system, and digestive tract exit; opposite to the back or dorsal side. The characteristic body curvature of resting or killed nematodes is almost always ventrad (Figs. 17, 45, 60).

ventromedially Situated or occurring in the medial ventral line.

vermiform Worm-shaped; a descriptive term characterizing the form of members of the phylum Nematoda; cylindrical nematodes that narrow to varying degrees toward the head and tail ends (Figs. 16, 33, 45, 52, 60).

vestibule extension An expanded extension of the vestibule lining of varying size and shape (Figs. 4*C*, 61*C*, 80*C*) lined by thin stomatal cuticle, which posteriorly subtends and attaches to the stylet shaft.

vestibule (*also* stoma) Mouth cavity, bounded by the central tube of the head skeleton in nematodes with stylets and originating from components of the body cuticle. *See* head skeleton.

villi (*also* microvilli) Small, tubular projections of the intestinal lining that extend into the lumen (Fig. 10*A*, *D*); inconspicuous in most nematodes and of no diagnostic value.

vulva The external, usually transverse opening (gonopore) of the female reproductive system, which is lined by invaginated body cuticle (Figs. 16, 21*C*, 34*A*). By contrast, the cuticular lining of the vagina, although continuous with the body cuticle lining the vulva, is modified in structure.

vulva bridge In ambifenestrated cysts, the vulva margins (lips) persist during the development and fenestration of the cyst, forming a transverse "bridge" bisecting the fenestrae (Fig. 66*D*).

vulva cone The posterior protuberance or cone top of a female cyst of *Heterodera* (Fig. 66*B*, *C*).

vulva fenestra A thin transparent zone in the body wall of a white female and particularly in the cyst wall. The vulva fenestra encircles or is at the sides of the vulva (Figs. 66*D*; 68*D*; 69*C*; 70*B*, *C*). *See also* fenestra.

vulval membranes (*also* vulval flaps) Thin, bursa-like folds of cuticle along the lateral sides of a transverse vulva; a peculiarity of species of *Paratylenchus* (Fig. 19*C*) and *Aglenchus* (Fig. 41*D*).

white female The adult egg-laying stage of the cyst nematodes (Fig. 66*A*, *C*) preceding the cyst stage. The white female stage has particular diagnostic value for species of *Globodera* (Fig. 68*A*). The white female is comparable to the definitive stage in the root-knot nematode, which does not transform into a cyst.

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